

INTRODUCTION

Field work on the Amazonian slopes of the Andes in southern Colombia and Ecuador has revealed, and continues to reveal, a rich anuran fauna. Among the 124 species of frogs now known from elevations of 1000-3000 m on the Amazonian slopes in Ecuador, 12 belong to the dendrobatid genus *Colostethus*, 12 to the centrolenid genus *Centrolenella*, and 50 to the genus *Eleutherodactylus*. Frogs of the genus *Eleutherodactylus* have served as an impediment to summaries or checklists of the Ecuadorian amphibian fauna. Although some species probably remain to be discovered, we approach a working knowledge of the fauna after a decade of field work. The eleutherodactyline fauna of the Amazonian lowlands seems to be mostly known (Duellman, 1978; Lynch, 1980). Lynch (1979a) summarized the eleutherodactyline fauna of the southern Andes of Ecuador, including several of the species found on the Amazonian slopes.

In this paper we address 45 species of *Eleutherodactylus* found at elevations of 1000-3000 m on the Amazonian slopes of the Andes in Ecuador. Records also are given for those same species on the adjacent slopes in Colombia; in so doing we list more than 2800 specimens examined. The elevational limits essentially correspond to the boundaries of the lowland tropical rainforest and the páramo. We are concerned with the frogs inhabiting the montane rainforest or cloud forest. These altitudinal limits appear to have biological significance in that only eight of the 45 species descend below 1000 m in Ecuador; five of these are actually lowland species that ascend the slopes into the cloud forest. Seven species also occur above 3000 m; one of those is primarily a highland species that descends into montane forest.

Twelve of the 45 species are named as new. We also report and describe *E. pastazensis* Andersson, *E. rubicundus*

(Jiménez de la Espada), and *E. trachyblepharis* (Boulenger), none of which has been mentioned in the literature (except in checklists) since their original descriptions. Not included in this report are *E. buckleyi* (Boulenger), which descends into upper montane forest near El Carmelo (east of Tulcán, Ecuador), or a species presently confused with *E. vertebralis* (Boulenger), also from the El Carmelo area. *Eleutherodactylus buckleyi* occurs primarily in páramo and will be treated by Lynch in an account of the frogs of the northern Andes of Ecuador. The other species is widespread in the Colombian Andes, but a systematic summary is postponed pending re-examination of the complex of frogs now called *E. vertebralis*. *Eleutherodactylus chalceus* (Peters), a name long associated with the Amazonian slopes and lowlands, will be shown by Lynch (ms) to be identified with a species on the Pacific slopes and lowlands.

As part of our systematic treatment of the frogs, we present a discussion of taxonomic characters in the genus *Eleutherodactylus* and a key to the identification of the species on the Amazonian slopes of the Andes in Ecuador. In an attempt to summarize our knowledge of these frogs in the region, we provide discussions of the distribution of the species and of the eleutherodactyline communities. The appendices include a list of specimens examined and a gazetteer of localities from which specimens of *Eleutherodactylus* were collected.

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Specimens are identified in the text by museum number and an acronym for the collection or institution. We have used the acronyms suggested by Duellman et al. (1978).

AMNH	American Museum of Natural History, New York
ANSP	Academy of Natural Sciences, Philadelphia
BM	British Museum (Natural History), London
CAS-SU	Stanford University collection; housed at California Academy of Sciences, San Francisco
EP	Eugenia del Pino collection, Universidad Católica, Quito, Ecuador
GOV	Gustavo Orcés V. collection, to be catalogued at USNM
JAP	James A. Peters collection, to be catalogued at USNM
KU	University of Kansas Museum of Natural History, Lawrence
LSUMZ	Louisiana State University Museum of Zoology, Baton Rouge
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge
MRHN	Institut Royal des Sciences Naturelles de Belgique, Brussels
MSNT	Museo Civico di Storia Naturale de Torino, Torino
NHMG	Naturhistoriska Museet, Göteborg
SMF	Natur-Museum Senckenberg, Frankfurt-am-Main

UIMNH	University of Illinois Museum of Natural History, Urbana	USNM	National Museum of Natural History, Washington, D.C.
UMMZ	University of Michigan Museum of Zoology, Ann Arbor	WCAB	Werner C. A. Bokermann collection, São Paulo, Brasil

SYSTEMATICS

Frogs of the genus *Eleutherodactylus* are notorious for their taxonomic difficulty. This stems in large part from the sheer size of the genus—we estimate more than 400 species are now recognized—but also because development and discussion of taxonomically useful characteristics has been slower than descriptions of species. In addition to the descriptions provided below with their comparable diagnoses, we provide a discussion of the taxonomic characteristics and a key to the species found on the Amazonian slopes of the Andes. Lastly, a synopsis of the taxonomic relationships is provided even though the synopsis is far from complete—it represents our judgments at this stage of the assessment of this large genus.

TAXONOMIC CHARACTERISTICS

Measurements and abbreviations employed are as follows: snout-vent length (SVL)—distance from tip of snout to vent; shank—measured on flexed hind leg from knee to heel, including only tibiofibula; head width (HW)—greatest width of head, usually at level of anterior edge of tympanum; head length—head length, estimation of distance from snout tip to line between ricti (not direct measure of distance between snout tip and rictus as employed by Zweifel, 1955); upper eyelid width—distance between outer edge of upper eyelid and inner margin of eye bulge, approximately perpendicular to margin of jaw (not measurable if eye retracted); interorbital distance (IOD)—shortest distance between eyes across braincase (not a measure of braincase width, which is usually shorter); eye length—distance between anterior and posterior corners

of eye (difficult to measure if eye is retracted); tympanum length—distance from anterior edge of tympanic annulus to posterior edge of annulus; eye to nostril distance (E-N)—distance between posterior edge of nostril and anterior edge of eye (usually reflects snout length). Reported values for measurements and proportions normally include the range of values, mean, and number of values. In some cases, two standard errors of the mean are also reported (e.g., $\bar{x} = 34.8 \pm 2.6$).

The order in which characteristics are addressed corresponds to that employed in the diagnosis. The sequence has been employed by JDL for the past ten years; the logic for the particular sequence has been forgotten, but generally follows JDL's search pattern when examining frogs, *viz.*, general texture of skin, condition of tympanum, head shape, traits within the mouth, structure of hands, structure of feet, color pattern, and size.

Skin texture.—The skin of the venter is smooth or bearing wrinkles in members of the *biporcatus*, *discoidalis*, and *fitzingeri* groups but is granular (areolate) in members of the *unistrigatus* group. *Eleutherodactylus galdi* (Jiménez de la Espada) has areolate skin on the venter but also has larger more prominent warts scattered on the belly. *Eleutherodactylus rubicundus* has finely areolate skin on the venter; the granules are usually not visible without magnification. The throat is smooth (or wrinkled) in all taxa.

Many eleutherodactyline are readily sorted using the array of features generally described as being part of the texture of the skin of the dorsum. Dor-

solateral folds are evident in several members of the *fitzingeri* group as well as in high montane species of the *unistrigatus* group. Such folds extend from above the tympanum to a point above the groin. In *E. conspicillatus* (Günther) and *E. peruvianus* (Melin) the folds are series of closely packed warts arranged in a line.

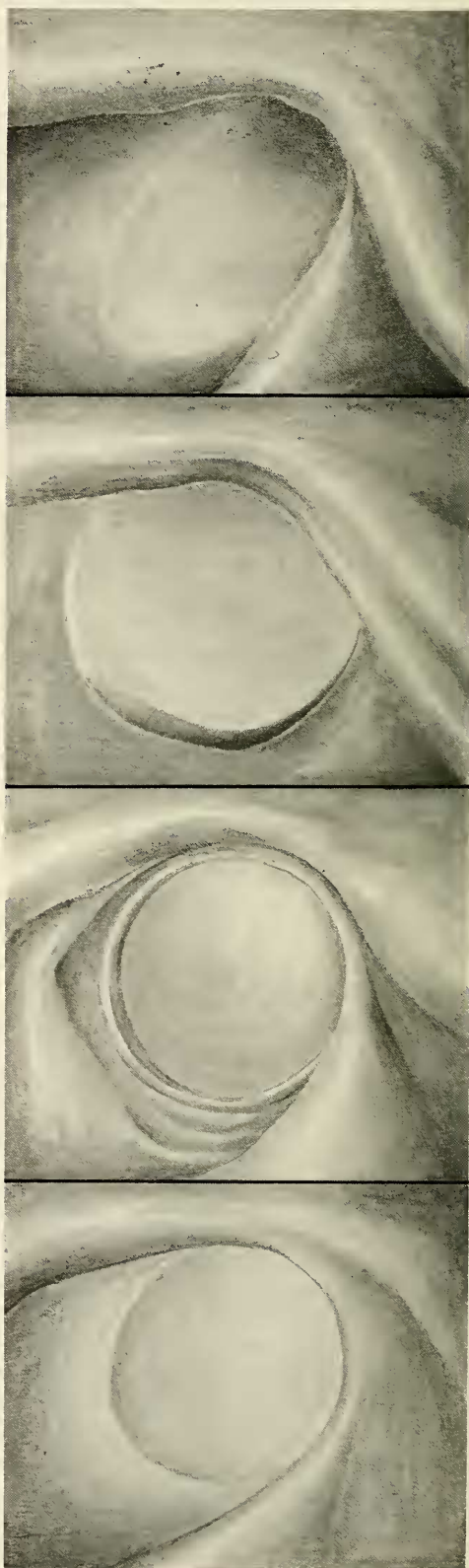
The paravertebral folds of *E. chloronotus* Lynch are sinuous and may represent extensions of occipital folds (or rows of tubercles) seen in many eleutherodactylines. The occipital folds are frequently accented with W-shaped dark (or pale) markings. The system of folds and ridges of *E. cornutus* (Jiménez de la Espada) includes a H-shaped occipital fold as well as many short folds arranged in a complex but repeated pattern; initial perception of the skin of *E. cornutus* is that it is tuberculate.

The skin between whatever folds and/or enlarged warts on the back ranges from perfectly smooth (even under magnification), to finely shagreened (tiny, uniform-sized granules), to shagreened (larger granules, sometimes visible without magnification, but not pungent), to tuberculate or spinous (large, pungent granules). Our characterizations of skin texture take the form of one of these states plus an attempt to describe whatever folds and enlarged warts are present.

Some enlarged tubercles are more obvious. Enlarged warts on the upper eyelid, between the eyes, or on the forearm, knee, heel, and tarsus are usually noted in connection with traits other than skin texture (see below).

Tympanum.—Most species of *Eleutherodactylus* have complete ears (tympanic annulus, *cavum tympanicum*, *plectrum*), but one species on the northern Amazonian slopes lacks all of these fea-

FIG. 1.—Tympanum concealment in *Eleutherodactylus*. Top to bottom: *E. quaquaverus*, KU 123749; *E. incomptus*, KU 165844; *E. prolatus*, KU 146165; *E. eriphus*, KU 155451. Left side of head is illustrated without color pattern or tubercles.



tures (*E. pugnax* Lynch). Many other species have complete but concealed ears, which sometimes may be detected in desiccated individuals. When the tympana are visible (Fig. 1), care must be taken to recognize the state in which the tympanum is visible through thin skin (= partially visible) as different from the case in most frogs having a visible tympanum (the raised annulus is visible along at least the anterior, ventral, and part of the posterior margins of the tympanum; the upper border of the annulus is normally obscured by the supratympanic fold—extending from the eye, above the ear, to above the insertion of the forearm). Relatively few taxa may be distinguished on the basis of tympanum size; the distinguishing ability is further hampered by shape differences between sexes (usually more round in males, higher than long in females).

Head shape.—Rivero (1961) described character-states for snout shape in Venezuelan frogs. The *Eleutherodactylus* on the Amazonian slopes exhibit acuminate, subacuminate, ovoid, and rounded snouts (as seen in dorsal view). In lateral profile, fewer variations are considered modes (rounded, acutely rounded, truncate, and protruding); Lynch (1974) provided illustrations for some of these based on species found in the Amazonian lowlands. Many species have a papillum on the tip of the snout changing the aspect of snout shape.

Rivero (1961) also diagramed differences in the shape of the canthus rostralis. The canthus rostralis is sharp (approximately 100°) and either straight, weakly concave, or weakly convex in most species of the *fitzingeri* group; this character-state is usually correlated with the loreal region sloping abruptly to the lips. In those frogs in which the loreal region slopes gradually to the lips, the canthus rostralis is less sharp (obtuse) but sufficiently distinct to allow characterization as concave or convex. Rounded canthi rostrali consti-

tute the other extreme in which the canthus is obsolete.

In relatively few *Eleutherodactylus* (but in many members of the *unistri-gatus* group on the northern Amazonian slopes), the lips are flared. The flaring is pronounced in the broad-headed frogs of the *sulcatus* group and in *E. cruentus* (Peters) and *E. latidiscus* (Boulenger) from trans-Andean South America. Frogs having flared lips have gently sloping loreal regions and/or flaring evident below and posterior to the eyes.

Traits of the mouth.—On the roof of the mouth, the sizes and relative positions of the choanae and vomerine odontophores are the principal characteristics. The choanae are usually not concealed by the palatal shelf of the maxillary arch (condition seen in all Amazonian slope taxa). The choanae are of various sizes, and size is normally referenced to the size of the frog rather than to the vomerine odontophores.

The vomerine odontophores (if present) are well posteriad to the choanae and, in all taxa except the members of the *biporcatus* and *discoidalis* groups, well medial to the choanae as well. In the exceptions, the lateral edge of the odontophore extends to the level of the choanae. The shapes of the odontophores are triangular, broad (or arched), round, oval, or oblique. Oblique odontophores are arranged directed medio-posteriorly; the most medial (or posterior) component is of the greatest elevation. The teeth on the odontophores assume transverse, slanted, or clumped distributions (correlated with triangular and broad, oblique, and round or oval shapes). Odontophore size is expressed relative to the size of the choanae.

Tongue shape has been used in frog identification for more than a century but is of relatively little value (as expressed by failure to include it in the numbered traits). The degree of attachment of the tongue and presence or absence of a notch along the posterior border appears to be of some, although limited, value in species separation.

Adult males are often recognized as adults on the basis of the presence of vocal slits posterolateral to the tongue and/or the presence of an external vocal sac. However, many species of *Eleutherodactylus* lack both vocal slits and external vocal sacs. Few variations in the form of the vocal sacs are expressed in *Eleutherodactylus*; *E. crenunguis* Lynch from the Pacific versant in Ecuador has weakly bilobed vocal sacs and several high altitude species apparently have internal vocal sacs.

Structure of the hands.—The posterior border of the forelimb may bear conical (or in some cases elongate, e.g., *E. inusitatus*) tubercles. Most species have an antebrachial tubercle but relatively fewer have a complete series of tubercles along the forearm (ulnar tubercles). The ulnar tubercles may coalesce forming a scalloped ridge (as in *E. cornutus*) but are normally discrete.

The large tubercles on the palm include an inner thenar tubercle on the thumb (normally considerably smaller than the lateral palmar tubercle). The palmar tubercle is bifid (or cordiform) in all of the Andean slope *Eleutherodactylus* but in other species of the genus there is a round palmar tubercle (*E. zeuctotylus* Lynch and Hoogmoed) or divided palmar tubercles wherein the bifid palmar is in two distinct elements. The remaining palmar surface may bear supernumerary palmar tubercles. These are normally non-pungent and sometimes difficult to see. They are smaller than the subarticular tubercles and the thenar and palmar tubercles, which are more elevated.

The subarticular tubercles are the most prominent tubercles on the ventral surface of the manus. The inner two fingers each have one tubercle whereas each of the outer two fingers has two tubercles. The tubercles are round or elongate or, more rarely, broader than long. In most eleutherodactylines the subarticular tubercles are pungent (elevated), but in some species they are flattened and in others are conical.

In many *Eleutherodactylus* the lateral margins of the digits bear keels or fringes. In no case are the fringes comparable to those seen in elosine leptodactylids. The fingers develop false keels or fringes if the specimen is allowed to desiccate, so some care must be exercised in the use of this character. Fringes are easily seen but the states "keeled" and "lacking keels or fringes" are more difficult to distinguish. If the digit is rotated during examination under magnification, the keel becomes apparent. However, it is desirable to inspect several fingers along their entire margins to gain certainty. If the pad is collapsed, the keels are probably due to desiccation.

All *Eleutherodactylus* bear discs on the ventral surfaces of the digit tips of at least the toes regardless of whether or not the digit is expanded to form a pad. Some species lack discs on one or more fingers of the hand. Lynch (1975a) reported the absence of finger discs in *E. sulcatus* (Cope) and (1976a) the loss of some discs (inner fingers) in the *pyrrhomerus* assembly (*unistrigatus* group). The discs are normally broader than long but in many species having narrow pads are as long as wide (see Lynch 1976b, 1978).

Pad size is subject to greater variation than discs size (or presence). The digital pads may be apically rounded (most), emarginate, notched, or pointed. Normally, the pad of the thumb is not developed or only slightly broader than the digit below the disc whereas the pads of fingers II, III, and IV are readily seen and those of III and IV normally larger than that of II. However, the fingers of *E. dolops*, *E. elassodiscus*, and *E. nigrovittatus* (among Amazonian slope species) lack pads on the fingers.

The relative lengths of the inner two fingers was used by Lynch (1976b) to separate some species groups. Frogs of the *unistigatus* group (abundant on the Amazonian versant) have the first finger shorter than the second, whereas frogs of the *biporcatus*, *discoidalis*, and *fitz-*

ingeri groups have the first finger longer than the second. To record this trait, the inner two fingers must be adressed equally; if one is adressed against the other, finger lengths may not be correctly determined.

Males of many *Eleutherodactylus* have non-spinous, white (or cream) nuptial pads on the thumbs. The pad is distinctly glandular in some species but not in all. Many other species lack this secondary sex feature. Although Taylor (1952), Rivero (1968), and Lynch (1970a) cited the feature, it remained for Savage (1975) to point out its taxonomic utility and frequency.

Structure of the foot and tarsus.—The heel may lack tubercles or may bear obvious but non-conical tubercles, one or more conical tubercles, or a single elongate tubercle or calcar. The outer edge of the tarsus usually bears two to four non-conical or more rarely conical tubercles if there is a conical tubercle on the heel. The tubercles rarely continue along the outer edge of the foot and toe V (but are sometimes replaced by a ridge).

The inner edge of the tarsus normally lacks tubercles or folds, but some species have a single tubercle somewhere along the distal one-half of the tarsus. Other species have a low ridge in place of the tubercle (usually in contact with the inner metatarsal tubercle). The least common variation is the presence of a fold on the inner edge of the tarsus (normally on the distal one-half only).

All *Eleutherodactylus* have two metatarsal tubercles; the inner is normally larger and longer than wide, whereas the outer is usually round in outline. The inner metatarsal tubercle is described as oval (length twice width) or elongate (length three times width). The outer metatarsal tubercle is described in terms of the size of the inner and in a few *Eleutherodactylus* is as large as the inner. Supernumerary plantar tubercles may be entirely absent but most species have some. These tubercles are low (non-pungent) and smaller than

the smallest subarticular tubercle. Frogs may have only two to four tubercles (proximal to the basal subarticular tubercles of toes II-IV) or may have the entire plantar surface tuberculate. In a few frogs, the plantar tubercles are more prominent (*E. sulcatus*, *Hylactophryne*, and *Ischnocnema*). The subarticular tubercles of the toes are like those of the fingers except that the inner two toes each have one tubercle, the third and fifth two each, and the fourth three.

The toes may or may not have lateral fringes or lateral keels. Although most species of the genus lack webbing, some *Eleutherodactylus* (*karlschmidti* and two unnamed species) have nearly complete toe webbing and the free phalanges bear prominent lateral fringes to the base of the discs. In these (and some other species as well) prominent lateral fringes occur on the outer edge of toe V and the inner edge of toe I. The discs and pads of the toes exhibit comparable variation to that seen on the fingers except that the variation in pad sizes among the five toes is less pronounced.

Size and proportions.—South American *Eleutherodactylus* range in size from the diminutive *E. trachyblepharis* (males 12.1-15.8, \bar{x} = 13.8 mm SVL) to a series of large, broad-headed species (adult females of *E. anomalus*, *E. biporcatus*, *E. bufoniformis*, and *E. necerus* exceed 95 mm SVL). On the Amazonian versant of the Andes the largest species probably do not exceed 70 mm (*E. condor* and *E. cornutus*).

Many otherwise similar species pairs may be discriminated easily on the basis of body size. Adult male *Eleutherodactylus* are distinguished from juvenile males on the basis of having vocal slits and sacs (some species), non-spinous nuptial pads on swollen thumbs (some species), or enlarged testes. In some species, the testes are black or reticulated with brown in adults. Adult females are distinguished from juveniles on the basis of enlarged convoluted oviducts and, if mature eggs are present, large, yellow ovarian eggs. Sexual di-

morphism in body size is pronounced in the genus. Thirty-two species found on the Amazonian versant of the Andes in southern Colombia and northern Ecuador (south to the Río Pastaza) exhibit dimorphisms (female \bar{x} /male \bar{x}) ranging from 1.25 (*E. elassodiscus*, *E. trachyblepharis*, *E. trepidotus*) to 1.77 (*E. lividus*). The 15 species found on the Amazonian versant in southern Ecuador exhibit dimorphisms ranging from 1.18 (*E. proserpens*) to at least 1.73 (*E. condor*). Twenty-four species from the Amazonian lowlands exhibit dimorphisms ranging from 1.20 (*E. paululus*) to 1.97 (*E. sulcatus*). The degree of di-

morphism is not different among the three areas (mean, ± 2 standard errors, and N for the three areas respectively are 1.41 ± 0.05 , 32; 1.42 ± 0.09 , 15; and 1.42 ± 0.07 , 24). Size data for the 36 species found on the northern Amazonian versant are given in Table 1, for the 16 species found on the southern Amazonian versant in Table 2, and for the 24 species found in the Amazonian lowlands in Table 3.

The only proportion suggested to be taxonomically significant is head width (Lynch, 1975a). With the exception of *E. cornutus* (a broad-headed species), all of the Amazonian versant frogs have

TABLE 1.—Body sizes of *Eleutherodactylus* found on the northern Amazonian Andean versant in Ecuador. Values include range (mean ± 2 standard errors) sample size.

Species	Males	Females	Dimorphism
<i>E. acerus</i>	25.0-34.0(30.2)3	45.1	1.49
<i>E. chloronotus</i>	22.9-30.3(26.4 \pm 0.9)25	31.9-38.9(35.9 \pm 1.1)14	1.36
<i>E. cornutus</i>	35.5-43.0(39.2)2	> 54.0	-----
<i>E. cremnobates</i>	28.4-32.5(30.6 \pm 1.3)7	41.6-51.7(46.2 \pm 2.6)8	1.51
<i>E. devillei</i>	19.6-31.6(26.8 \pm 1.2)26	34.7-44.7(39.0 \pm 0.9)26	1.46
<i>E. dolops</i>	35.8-40.3(38.0)2	56.6-57.6(57.1)3	1.50
<i>E. elassodiscus</i>	22.0-29.2(26.9 \pm 1.1)14	29.7-36.9(33.6 \pm 1.1)16	1.25
<i>E. eriphus</i>	18.1-25.2(21.1 \pm 1.6)9	25.8-29.0(27.4)2	1.30
<i>E. galdi</i>	17.1-24.8(21.0 \pm 1.7)8	28.1-34.0(31.7 \pm 1.6)9	1.51
<i>E. gladiator</i>	14.9-15.8(15.2)3	> 16.0	-----
<i>E. glandulosus</i>	24.2-30.2(26.6 \pm 0.6)27	31.8-41.3(36.1 \pm 0.9)20	1.36
<i>E. ignicolor</i>	18.0	26.4	1.47
<i>E. incanus</i>	14.9-19.4(17.5 \pm 1.1)9	23.9-30.6(29.2 \pm 1.2)5	1.67
<i>E. incomptus</i>	15.6-18.8(17.5 \pm 0.7)10	23.7-25.9(24.5 \pm 0.6)7	1.40
<i>E. inusitatus</i>	-----	24.0-24.4(24.2)2	-----
<i>E. lacrimosus</i> ¹	19.6-23.7(21.0 \pm 0.8)11	24.4-32.5(27.0 \pm 3.0)5	1.28
<i>E. lanthanites</i> ¹	23.8-27.9(26.3 \pm 1.6)5	38.7-45.4(41.2)4	1.57
<i>E. leoni</i>	13.0-18.3(16.5 \pm 1.0)11	19.7-25.0(21.9 \pm 0.6)26	1.33
<i>E. leucopus</i>	30.0-37.8(33.3 \pm 1.0)18	42.3-44.0(42.9)3	1.29
<i>E. lividus</i>	18.2-20.4(19.3)2	32.9-35.0(34.1)3	1.77
<i>E. nigrogriseus</i>	19.3-26.0(22.7 \pm 0.9)20	28.5-30.2(29.2)4	1.29
<i>E. nigrovittatus</i> ¹	17.2-24.6(21.4 \pm 0.6)33	25.0-30.5(27.4 \pm 1.7)21	1.28
<i>E. pastazensis</i>	19.5	30.9-31.7(31.3)2	1.60
<i>E. peruvianus</i> ²	29.2-35.8(31.8 \pm 1.4)10	38.6-46.4(42.3 \pm 1.4)10	1.33
<i>E. petersi</i> ²	14.5-19.9(17.2 \pm 0.5)35	20.3-23.1(21.6 \pm 0.7)8	1.26
<i>E. prolatus</i>	13.7-18.4(16.8 \pm 0.5)20	20.8-24.1(22.3 \pm 0.8)9	1.33
<i>E. pugnax</i>	22.1-28.0(25.0)2	30.8-33.2(32.0)2	1.28
<i>E. quaquaversus</i>	19.6-22.5(20.7 \pm 0.4)29	24.6-31.3(27.3 \pm 0.8)20	1.32
<i>E. rubicundus</i>	31.4-35.6(32.9 \pm 1.5)5	46.5-51.2(48.8)2	1.48
<i>E. trachyblepharis</i>	12.1-15.8(13.8 \pm 0.4)20	15.8-19.2(17.2 \pm 0.4)19	1.25
<i>E. trepidotus</i>	14.4-21.3(16.9 \pm 2.5)5	17.3-25.5(21.2 \pm 1.0)21	1.25
<i>E. unistrigatus</i>	14.9-23.4(18.8 \pm 0.8)25	23.3-30.8(26.3 \pm 0.4)46	1.40
<i>E. ventrimarmoratus</i>	17.8-25.5(21.8 \pm 1.8)8	33.3-43.8(36.9 \pm 1.9)9	1.69
<i>E. w-nigrum</i>	29.3-46.8(34.3 \pm 1.2)32	44.4-56.6(49.9 \pm 1.9)16	1.45

¹ Amazonian slope populations consist of larger frogs than those from the Amazon Basin (see Table 3).

² Not including specimens from Baños and vicinity; see Table 4.

TABLE 2.—Body sizes of *Eleutherodactylus* found only on the southern Andean slopes of the Amazonian versant. Values: range ($\bar{x} \pm 2SE$) N.

Species	Males	Females	Dimorphism
<i>E. atratus</i>	17.4-24.0(21.7 \pm 1.7)19	24.9-29.2(27.4 \pm 1.3)10	1.26
<i>E. baryecus</i>	27.2-30.4(29.0)5	38.2-43.5(40.8 \pm 1.3)8	1.41
<i>E. bromeliaceus</i>	16.7-22.8(20.8 \pm 0.9)15	23.0-28.5(26.6 \pm 1.6)6	1.28
<i>E. colodactylus</i>	14.0-20.7(17.1 \pm 0.5)46	16.5-25.8(20.8 \pm 0.8)33	1.22
<i>E. condor</i>	32.1-39.5(36.5 \pm 1.7)9	63.2	1.73
<i>E. cryptomelas</i>	28.2-30.3(29.2)4	38.6	1.32
<i>E. proserpens</i>	15.2-21.0(18.6 \pm 1.0)11	20.2-23.5(22.0)4	1.18
<i>E. pycnodermis</i>	18.0-32.3(25.1 \pm 1.4)30	32.5-44.4(38.0 \pm 1.1)40	1.51
<i>E. spinosus</i>	16.1-25.0(20.1 \pm 0.6)34	28.3-34.5(31.8 \pm 0.6)29	1.58
<i>E. w-nigrum</i> ¹	28.4-45.1(36.7 \pm 1.0)55	53.0-65.4(59.2 \pm 2.6)9	1.61

¹ Specimens from the northern Amazonian slopes are significantly different in size (Table 1).

TABLE 3.—Body sizes of *Eleutherodactylus*¹ found in the Amazon Basin in Brasil, Colombia, Ecuador, and Perú. Values: range ($\bar{x} \pm 2SE$) N.

Species	Males	Females	Dimorphism
<i>E. acuminatus</i>	17.1-22.6(19.4 \pm 0.8)14	25.6-31.3(28.0 \pm 1.0)14	1.44
<i>E. altamazonicus</i>	14.4-23.1(18.8 \pm 0.8)28	23.6-33.9(27.9 \pm 0.8)42	1.48
<i>E. carvalhoi</i>	13.5-14.8(14.2)2	16.3-24.0(20.0)6	1.41
<i>E. conspicillatus</i>	23.2-30.1(27.3 \pm 0.6)29	34.8-48.8(40.2 \pm 1.7)19	1.47
<i>E. croceoinguinis</i>	12.8-18.2(14.6 \pm 0.7)14	18.0-21.9(19.8 \pm 0.6)19	1.36
<i>E. diadematus</i>	21.4-27.4(23.5 \pm 0.8)15	35.4-44.5(39.8 \pm 1.2)19	1.69
<i>E. fenestratus</i>	23.8-34.3(28.3 \pm 0.9)29	34.0-50.0(41.4 \pm 1.5)32	1.46
<i>E. lacrimosus</i> ²	16.1-20.0(18.5 \pm 0.5)18	20.6-24.4(22.5 \pm 0.5)18	1.22
<i>E. lanthanites</i> ²	21.7-26.0(23.5 \pm 0.6)20	27.5-42.2(36.2 \pm 1.3)31	1.54
<i>E. malkini</i>	30.4-37.2(32.9 \pm 1.2)11	41.5-47.9(44.8 \pm 1.3)9	1.36
<i>E. martiae</i>	11.8-16.8(15.1 \pm 0.4)29	18.3-22.2(20.4 \pm 0.4)36	1.35
<i>E. nigrovittatus</i> ²	13.3-19.4(17.0 \pm 1.9)8	19.7-22.1(20.9 \pm 0.5)9	1.23
<i>E. ockendeni</i>	17.9-21.3(19.4 \pm 0.5)18	24.6-31.1(27.2 \pm 0.5)37	1.40
<i>E. orphnolaimus</i>	24.0	24.8-33.4(29.1)2	1.21
<i>E. paululus</i>	13.6-17.1(15.0 \pm 0.8)9	16.5-19.4(18.0)4	1.20
<i>E. peruvianus</i> ^{2, 3}	27.3-31.6(30.0 \pm 0.6)16	38.9-44.2(41.3 \pm 1.5)7	1.39
<i>E. platydactylus</i>	16.3-23.9(19.3 \pm 2.1)8	28.6-33.3(30.3 \pm 1.7)5	1.57
<i>E. pseudoacuminatus</i>	12.7-17.6(15.4 \pm 0.7)15	18.1-22.4(19.9 \pm 0.5)21	1.29
<i>E. sulcatus</i>	19.7-36.2(26.0 \pm 4.8)8	42.4-59.7(51.2 \pm 2.6)15	1.97
<i>E. variabilis</i>	13.7-17.5(16.3 \pm 0.4)26	20.0-25.3(22.8 \pm 0.5)30	1.69
<i>E. vilarsi</i>	22.7-31.5(27.2 \pm 1.5)10	33.0-43.9(39.2 \pm 1.0)33	1.44
<i>E. zeuctotylus</i>	20.4-29.6(25.5 \pm 1.1)20	30.5-43.3(37.0 \pm 1.2)32	1.45

¹ See Table 1 for data for *E. quaquaversus*, *E. trachylepharis*, and *E. ventrimarmoratus*.

² Amazon lowland populations consist of significantly smaller frogs than do slope populations (see Table 1).

³ Sample from Cusuime, Río Cusuime, Provincia Morona-Santiago, Ecuador, 320m; other Amazon Basin populations are still smaller in body size (see Lynch, 1980).

normal head widths (mean HW/SVL 0.320-0.425). *Eleutherodactylus cornutus* has a mean HW/SVL of 0.520.

KEY TO THE SPECIES

- 1. First finger longer than second; skin of venter smooth (finely tuberculate in *E. rubicundus*) 2
- First finger shorter than second; skin of venter coarsely areolate 10
- 2. Pads absent on fingers (finger tip not

- appreciably wider than digit below disc) 3
- Pads present on fingers II-IV 5
- 3. Pads of toes pointed; dorsolateral folds present, incomplete
 *E. nigrovittatus*
- Pads of toes rounded; dorsolateral folds absent 4
- 4. Metatarsal tubercles approximately equal in size; adults moderate sized (males 22.0-30.0 mm, females 30.0-

- 37.0 mm SVL) *E. elassodiscus*
 Inner metatarsal tubercle 4-8 times
 size of outer; adults large (males
 35.0-40.0 mm, females more than
 55.0 mm SVL) *E. dolops*
5. Upper eyelid bearing one or more
 elongate tubercles *E. cornutus*
 Upper eyelid lacking conical or elon-
 gate tubercles 6
6. Heel bearing a conical or elongate
 tubercle 7
 Heel lacking enlarged tubercles ... 8
7. Toes bearing narrow lateral fringes;
 gular stripe absent ... *E. rubicundus*
 Toes lacking lateral fringes; white
 gular stripe present ... *E. lanthanites*
8. Large black spots on anterior and
 posterior surfaces of thighs and on
 flanks *E. w-nigrum*
 Not so patterned on limbs and flanks
 9
9. Venter moderately to heavily
 blotched with brown: upper eyelid
 narrower than to as broad as IOD;
 dorsolateral folds indistinct; adult
 females more than 60 mm SVL
 *E. condor*
 Venter cream with brown flecks; up-
 per eyelid broader than IOD; dorso-
 lateral folds present, interrupted;
 adult females less than 50 mm SVL
 *E. peruvianus*
10. Heel bearing at least one conical or
 elongate tubercle 11
 Heel lacking tubercles, or if present,
 flattened (not conical) 22
11. Upper eyelid bearing one or more
 conical or elongate tubercle 12
 Upper eyelid lacking pungent tuber-
 cles 20
12. Forearm bearing conical ulnar tuber-
 cles along edge 13
 Forearm lacking ulnar tubercles (ex-
 cept antebrachial) 18
13. Skin of dorsum pustular, tuberculate,
 or bearing scattered tubercles 14
 Skin of dorsum shagreened or finely
 areolate (without enlarged tuber-
 cles) 17
14. Posterior surfaces of thighs unicolor
 (cream or black) 15
 Posterior surfaces of thighs bicolor
 (black and white) 16
15. Posterior surfaces of thighs black ...
 *E. cryptomelas*
 Posterior surfaces of thighs cream ...
 *E. galdi*
16. Posterior surfaces of thighs barred
 black and white *E. eriphus*
 Posterior surfaces of thighs black
 with white spots *E. spinosus*
17. Tubercle on elbow and heel elongate
 (calcar) *E. inusitatus*
 Tubercles on elbow and heel conical
 (not elongate) *E. lividus*
18. Dorsum bearing many low ridges;
 groin black *E. atratus*
 Dorsum shagreened or feebly warty,
 lacking many low ridges; groin not
 black 19
19. H-shaped folds on occiput; tympan-
 um not concealed *E. prolatus*
 No folds on occiput; tympanum con-
 cealed *E. quaquaversus*
20. Canthus rostralis sharp; tympanum
 distinct 21
 Canthus rostralis rounded; tympan-
 um partially concealed ... *E. incanus*
21. Posterior surface of thigh brown
 with large white spots
 *E. nigrogriseus*
 Posterior surface of thigh brown
 with cream flecks *E. rubicundus*
22. Tympanum and annulus absent or
 concealed 23
 Tympanic annulus evident external-
 ly and distinct (except dorsally) ... 29
23. Tympanum and annulus absent ... 24
 Tympanum and annulus concealed
 beneath skin 26
24. Canthus rostralis relatively sharp ...
 *E. baryecius*
 Canthus rostralis round 25
25. Vomerine odontophores absent
 *E. colodactylus*

- Vomerine odontophores present -----
 ----- *E. pugnax*
26. Canthus rostralis angular (moderately sharp) ----- 27
 Canthus rostralis round ----- 28
27. Upper eyelid lacking tubercles -----
 ----- *E. trachyblepharis*
 Upper eyelid bearing one or more conical tubercles ----- *E. leoni*
28. Venter white with black marbling -----
 ----- *E. ventrimarmoratus*
 Venter cream ----- *E. incomptus*
29. Canthus rostralis round ----- 30
 Canthus rostralis angular or sharp ----- 36
30. Venter black with white spots; pads scarcely developed ----- *E. trepidotus*
 Venter not spotted; pads small to large ----- 31
31. Skin of dorsum areolate -----
 ----- *E. proserpens*
 Skin of dorsum smooth to finely tuberculate ----- 32
32. Upper eyelid bearing one conical tubercle ----- *E. bromeliaceus*
 Upper eyelid lacking tubercles, or if present, tubercles flat ----- 33
33. Posterior surfaces of thighs dark brown ----- *E. cremnobates*
 Posterior surfaces of thighs pale, marbled or not with brown ----- 34
34. Skin of dorsum very finely shagreened ----- *E. lacrimosus*
 Skin of dorsum smooth bearing flat warts posteriorly ----- 35
35. Tip of snout bearing papilla -----
 ----- *E. pastazensis*
 Tip of snout lacking papilla -----
 ----- *E. unistrigatus*
36. Upper eyelid bearing one conical tubercle ----- *E. petersi*
 Upper eyelid lacking pungent tubercles ----- 37
37. Posterior surfaces of thighs uniform dark brown or bearing a large dark brown blotch ----- 38
 Posterior surfaces of thighs brown with large pale spots or barred with cream or colorless ----- 40
38. Large black blotch in groin -----
 ----- *E. pycnodermis*
 Groin not so marked ----- 39
39. Skin of dorsum smooth ----- *E. acerus*
 Skin of dorsum finely tuberculate with scattered warts ----- *E. leucopus*
40. Skin of dorsum bearing distinct folds or ridges ----- 41
 Skin of dorsum bearing warts but no ridges ----- 43
41. Two folds extending from occiput to above groin ----- 42
 Folds much shorter, more numerous -----
 ----- *E. gladiator*
42. Paravertebral folds sinuous; posterior surfaces of thighs barred -----
 ----- *E. chloronotus*
 Dorsolateral folds not sinuous; posterior surfaces of thighs yellow-brown with brown reticulation -----
 ----- *E. devillei*
43. Snout round in dorsal view; canthus rostralis concave ----- *E. glandulosus*
 Snout acuminate in dorsal view; canthus rostralis straight ----- *E. ignicolor*

ACCOUNTS OF THE SPECIES

In the following accounts we attempt to make comparable statements in the diagnoses and descriptions. The diagnoses consist of a series of 14 numbered statements (or set of statements) following the format used by Lynch (1979a). Following the numbered statements is a paragraph distinguishing the taxon from those it most nearly resembles (in our opinion). Measurements and proportions are given for each sex when the means differ significantly ($p \leq 0.05$); otherwise these data are combined.

Complete accounts are provided for each of the twelve new species as well as for *E. pastazensis*, *E. peruvianus*, *E. rubicundus*, and *E. trachyblepharis*. Abbreviated accounts (lacking descriptions) are provided for 19 species, and

very abbreviated accounts (only synonymies and brief remarks) are provided for eight species (*E. atratus*, *E. baryecuius*, *E. bromeliaceus*, *E. colodactylus*, *E. cryptomelas*, *E. proserpens*, *E. pycnodermis*, and *E. spinosus*) named by Lynch (1979a) and for *E. ockendeni* (recently treated by Lynch, 1974, 1980).

Eleutherodactylus acerus new species

Fig. 2A

Holotype.—KU 165471, adult female, taken 11 km ESE Papallacta, Provincia Napo, Ecuador, 2660 m, 22 March 1975 by William E. Duellman and Linda Trueb.

Paratypes.—KU 165472-73 collected at type-locality on 22 March and 27 April 1975 respectively; KU 143517, 7.8 km WNW Cuyujúa, Provincia Napo, Ecuador, 2750 m, 27 October 1971 by Bruce MacBryde.

Diagnosis.—1) skin of upper surfaces smooth, that of venter coarsely areolate; 2) tympanum distinct, its length $\frac{1}{2}$ – $\frac{2}{3}$ eye length; 3) snout subacuminate in dorsal view, pointed or protruding in lateral profile; canthus rostralis relatively sharp; 4) upper eyelid nearly as broad as IOD, lacking pungent tubercles; low cranial crests present; 5) vomerine odontophores prominent, round in outline; 6) males with vocal slits and subgular vocal sac, non-spinous nuptial pad on thumbs; 7) first finger shorter than second; fingers bearing large pads (largest on II–IV); discs broader than long; 8) fingers bearing ill-defined lateral fringes; 9) indefinite ridge of ulnar tubercles; 10) heel and tarsus lacking pungent tubercles; 11) two metatarsal tubercles, inner oval, 3–4 times size of outer; numerous supernumerary plantar tubercles; 12) toes bearing indistinct lateral keels, no webbing; toe pads smaller than those of outer fingers; 13) nearly black above, belly and undersides of limbs black, throat yellow-brown; posterior surface of thighs dark brown; 14) adults mod-

erate-sized, three males 25.0–34.0 mm, one female 45.1 mm SVL.

Eleutherodactylus acerus is most similar to *E. glandulosus* (Boulenger), *E. leucopus* Lynch, and *E. lividus* new species. *Eleutherodactylus glandulosus* has a rounded snout in lateral profile, and yellow spots on the flank, groin, anterior and posterior surfaces of the thighs, and concealed shank. *Eleutherodactylus leucopus* is probably the nearest relative of *E. acerus*; it differs in having small inner tarsal tubercles, faintly granular (not smooth) skin on the dorsal surfaces, and in having cream or white inner digits of the hands and feet. Both *E. acerus* and *E. leucopus* have protruding snouts; both are larger than *E. glandulosus*. *Eleutherodactylus lividus* (described below) differs from *E. acerus* in having a conical tubercle on the upper eyelid and similar tubercles along the outer edge of the tarsus and heel.

Description.—Head as wide as body, wider than long; head width 38.8–41.9 (\bar{x} = 39.8) percent SVL; snout subacuminate in dorsal view, pointed or protruding in lateral profile; snout short, E–N 82.9–90.0 (\bar{x} = 86.6) percent eye length; nostrils not protuberant, directed anterolaterally; canthus rostralis relatively sharp, weakly concave; loreal region weakly concave, sloping abruptly to lips; lips not flared; upper eyelid lacking tubercles (except in KU 143517, small conical tubercle on each eyelid), its width 81.2–100.0 (\bar{x} = 91.9) percent IOD; low cranial crests present along lateral edges of frontoparietals; tympanum directed dorsolaterally, prominent, round, its upper edge concealed by heavy supratympanic fold, separated from eye by distance 1.5 times tympanum length; tympanum length 36.4–42.6 (\bar{x} = 39.5) percent eye length; post-rietal tubercles small, round, subconical; choanae small, round, not concealed by palatal shelf of maxillary arch; vomerine odontophores median and posterior to choanae, separated by distance equal to a choanal width, round, elevated, each bearing clump of 4–5 teeth;

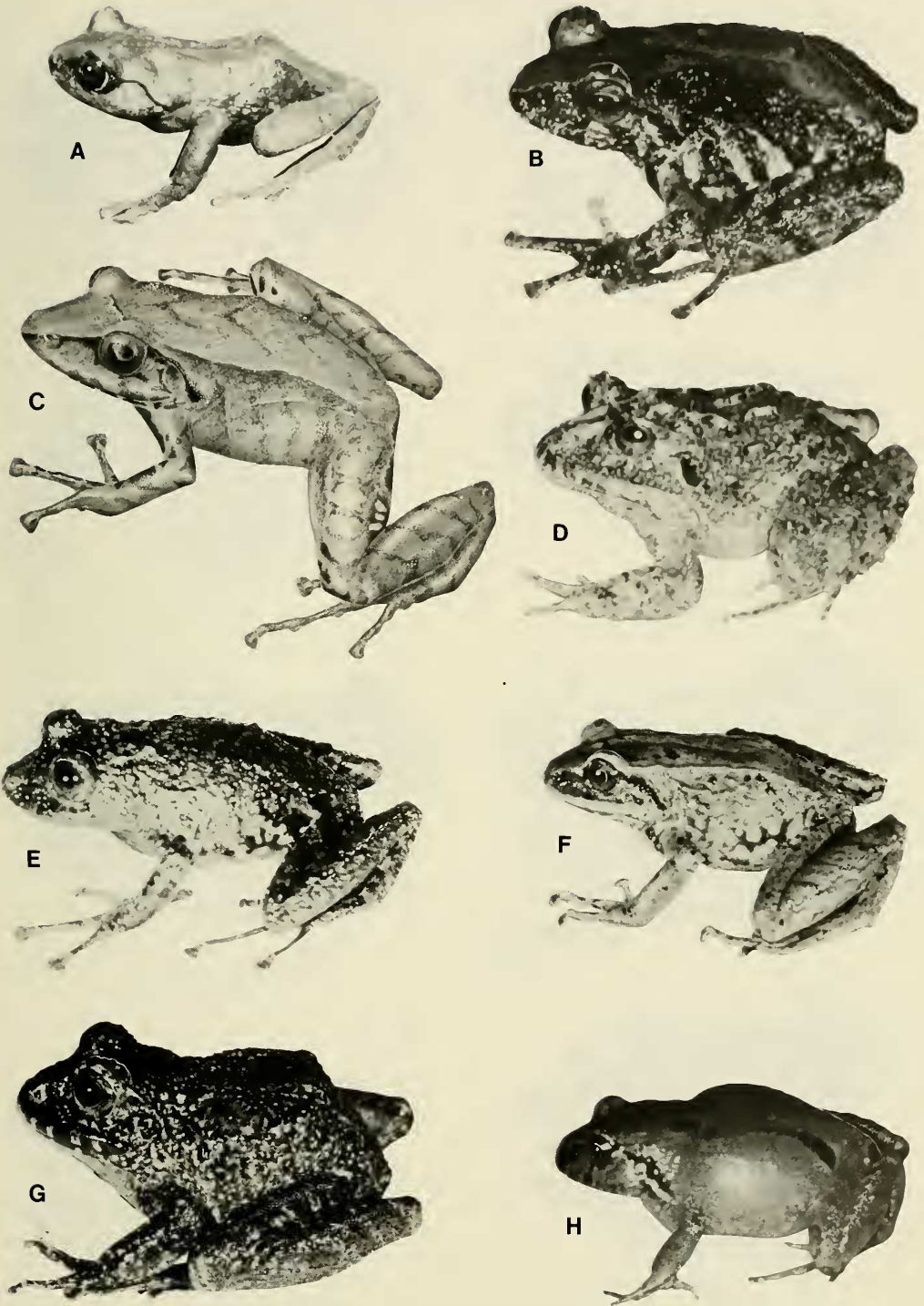


FIG. 2.—Andean *Eleutherodactylus*. A. *E. acerus*, KU 165471, adult female, 45.1 mm SVL. B. *E. chloronotus*, KU 143317, juvenile, 21.8 mm SVL. C. *E. condor*, KU 146992, immature female, 55.5 mm SVL. D. *E. cornutus*, KU 168009, adult male, 55.8 mm SVL. E. *E. cremnobates*, KU 143459, adult female, 41.6 mm SVL. F. *E. devillei*, KU 143401, adult female, 36.0 mm SVL. G. *E. dolops*, KU 143505, adult female, 57.6 mm SVL. H. *E. elassodiscus*, KU 168012, adult male, 23.1 mm SVL. C rendered by Linda Trueb; others from color transparencies by WED.

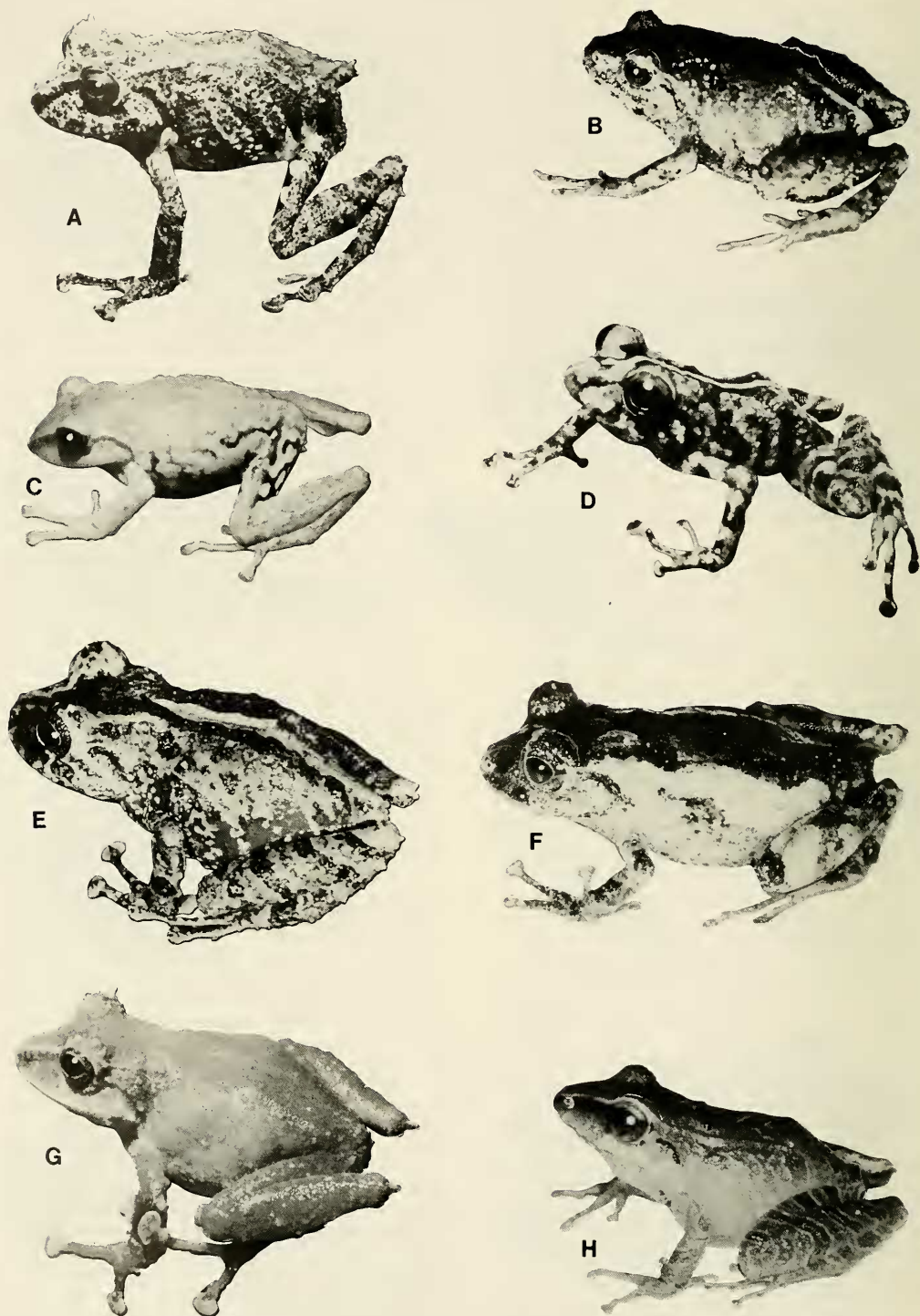


FIG. 3.—Andean *Eleutherodactylus*. A. *E. eriphus*, KU 166031, adult female, 29.0 mm SVL. B. *E. gladiator*, KU 143515, adult male, 14.9 mm SVL. C. *E. glandulosus*, KU 165435, adult male, 30.3 mm SVL. D. *E. ignicolor*, KU 165879, juvenile female, 21.1 mm SVL. E. *E. incanus*, KU 143458, adult female, 30.6 mm SVL. F. *E. incomptus*, KU 143492, adult female, 25.0 mm SVL. G. *E. inusitatus*, KU 166066, adult female, 24.0 mm SVL. H. *E. lanthanites*, KU 168834, juvenile, 23.6 mm SVL. From color transparencies by WED.

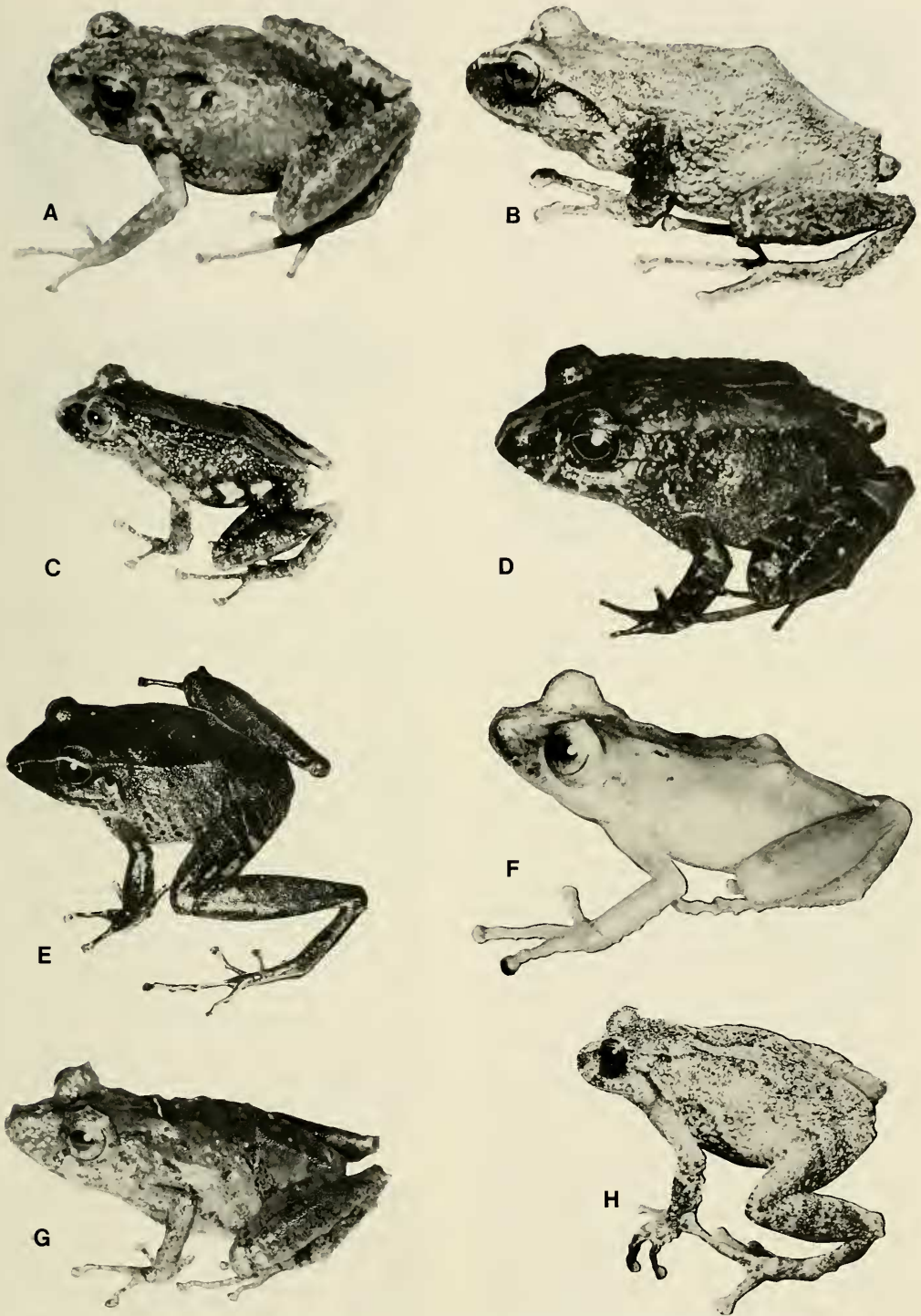


FIG. 4.—Andean *Eleutherodactylus*. A. *E. leoni*, KU 165897, adult female, 24.4 mm SVL. B. *E. lividus*, KU 166005, adult female, 35.0 mm SVL. C. *E. nigrogriseus*, KU 146109, adult female, 29.4 mm SVL. D. *E. nigrovittatus*, KU 123503. E. *E. peruvianus*, KU 123446, adult female, 49.0 mm SVL. F. *E. petersi*, KU 165993, juvenile female, 20.7 mm SVL. G. *E. prolatus*, KU 166008, adult female, 22.3 mm SVL. H. *E. pugnax*, KU 165561, immature female, 26.5 mm SVL. From color transparencies by WED.

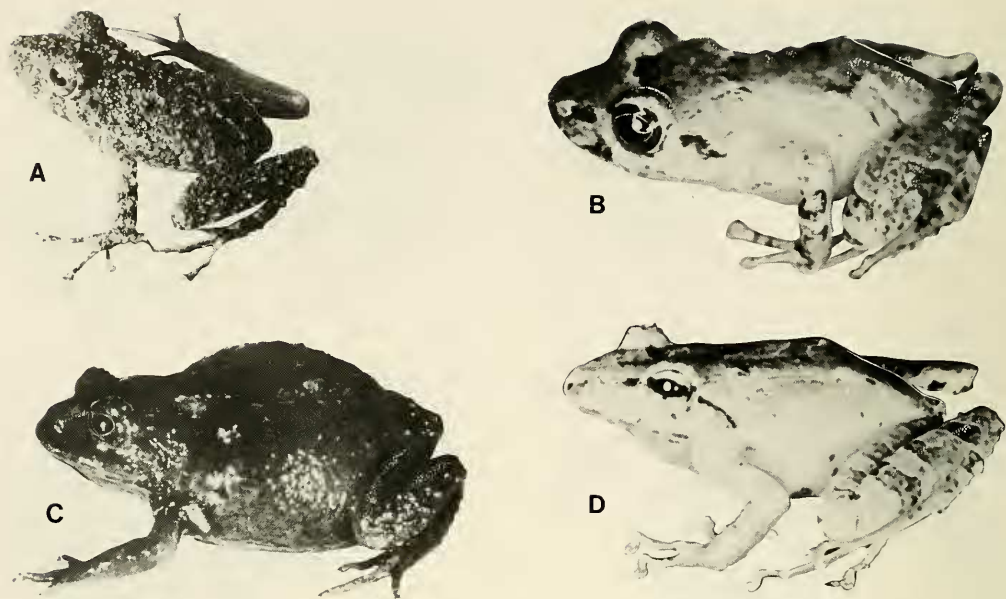


FIG. 5.—Andean *Eleutherodactylus*. A. *E. rubicundus*, KU 146170, adult male, 33.5 mm SVL. B. *E. trachylepharis*, KU 120180, adult female, 16.4 mm SVL. C. *E. trepidotus*, KU 143435, juvenile female, 15.8 mm SVL. D. *E. w-nigrum*, KU 143301, adult female, 50.3 mm SVL. From color transparencies by WED.

tongue longer than wide, posterior border feebly notched, posterior $\frac{1}{4}$ not adherent to floor of mouth; males with long vocal slits (from tongue to corner of jaw) and large subgular vocal sac.

Skin of dorsum, flanks, upper surfaces of limbs smooth, no dorsolateral folds, that of venter and undersides of thighs areolate; discoidal folds prominent, ending well anterior to groin; anal opening not extended, no para-anal warts; indefinite ridge of low ulnar tubercles; palmar tubercle bifid, nearly twice size of oval thenar tubercle; numerous supernumerary palmar tubercles, all non-pungent; subarticular tubercles round, non-conical, pungent; fingers bearing ill-defined lateral fringes, all with discs (broader than long) on dilated pads; pad of thumb as large as tympanum, those of fingers II–IV 1.5 times tympanum; thumb shorter than second finger; male with white, non-spinous nuptial pad on median surface of thumb.

Heel and tarsus lacking obvious tu-

bercles (inner tarsal tubercle evident in adult female KU 165471); inner metatarsal tubercle oval, length twice width; outer metatarsal tubercle subconical, length slightly greater than width, $\frac{1}{4}$ – $\frac{1}{2}$ size of inner; numerous supernumerary plantar tubercles, none prominent; subarticular tubercles round, subconical; lateral fringes on toes less obvious than those on fingers; toe discs broader than long on dilated pads, pads smaller than those on outer fingers, rounded apically; shank 45.0–52.7 (\bar{x} = 50.4) percent SVL; heels of flexed hind legs overlap; heel of adpressed hind leg reaches eye.

In preservative nearly black above; belly and undersides of limbs black or dark brown; throat yellow-brown to gray-brown; undersides of digits pale. KU 143517 is brown and the pale areas are pale golden-brown; the dorsum has a cream dorsoconcolor pattern (Lynch, 1966) with a brown patch extending from scapular to sacral regions.

Color in life.—Dorsum black or dark

gray; venter dark gray or dark grayish-brown; throat of male creamy brown; iris dark reddish-brown.

Measurements of holotype in mm.—SVL 45.1; shank 23.4; head width 18.9; head length 15.0; upper eyelid width 4.8; IOD 5.1; tympanum length 2.3; eye length 5.4; E-N 4.6.

Etymology.—Greek, in reference to the absence of tubercles on the eyelid, heel, and tarsus.

Distribution.—Known only from the type-locality and vicinity between Papallacta and Cuyujúa in upper montane cloud forest, 2660–2750 m.

Natural History.—One individual (KU 143417) was found by day under a log in a pasture (27 October 1971). The other three individuals were found at night on bushes (one at base, one 2 m above ground) on 22 March and 27 April 1975. The holotype (KU 165471) is a gravid female.

Remarks.—*Eleutherodactylus acerus*, *E. glandulosus*, *E. leucopus*, and *E. lividus* are a small constellation of species found in upper montane cloud forest in the valleys of the ríos Chingual and Papallacta in northwestern Provincia Napo, Ecuador. Lynch (1976c) suggested that *E. glandulosus* and *E. leucopus* were geminate species but it now appears more likely that *E. acerus* and *E. leucopus* enjoy that relationship and that *E. glandulosus* and *E. lividus* are less closely related.

Eleutherodactylus atratus Lynch

Eleutherodactylus atratus Lynch, 1979, Misc. Publ. Mus. Nat. Hist. Univ. Kansas 66:5 [Holotype.—USNM 199675, Suro Rancho, Provincia Morona-Santiago, Ecuador, 2683 m].

This species is found in subpáramo and cloud forests at elevations of 2195 to 2850 m on the Amazonian slopes of the Andes in southern Ecuador (Cordillera de Matanga to the Abra de Zamora) (Lynch, 1979a).

Eleutherodactylus baryecus Lynch

Eleutherodactylus baryecus Lynch, 1979, Misc.

Publ. Mus. Nat. Hist. Univ. Kansas 66:10 [Holotype.—USNM 199714, Suro Rancho, Provincia Morona-Santiago, Ecuador, 2683 m].

This species is found in subpáramo and cloud forests at elevations of 2195 to 2988 m on the Amazonian slopes of the Andes in southern Ecuador (Lynch, 1979a).

Eleutherodactylus bromeliaceus Lynch

Eleutherodactylus bromeliaceus Lynch, 1979, Misc. Publ. Mus. Nat. Hist. Univ. Kansas 66:12 [Holotype.—USNM 199731, from between Sapote and Suro Rancho, Provincia Morona-Santiago, Ecuador, 2622 m].

Lynch (1979a) reported specimens from cloud forests at elevations of 1707 to 2622 m on the Cordillera de Matanga in southern Ecuador. We have found additional specimens from the Cordillera del Condor and from the Cordillera de Zamora.

Eleutherodactylus chloronotus Lynch

Fig. 2B

Eleutherodactylus chloronotus Lynch, 1970, Journ. Herpetol. 3:140 [Holotype.—KU 117519, 3 km E Papallacta, Provincia Napo, Ecuador, 2900 m].

Diagnosis.—1) skin of dorsum smooth to feebly pustulate, pair of sinuous paravertebral folds present, no dorsolateral folds, that of venter coarsely areolate; 2) tympanum prominent, its length $\frac{1}{2}$ – $\frac{1}{2}$ that of eye; 3) snout subacuminate in dorsal view, angularly rounded or truncate in lateral profile; canthus rostralis sharp, strongly concave; 4) upper eyelid slightly narrower (to equal) than IOD, bearing small conical warts; no cranial crests; 5) vomerine odontophones small, oblique to subtriangular in outline; 6) males with vocal slits and subangular vocal sac; 7) first finger shorter than second; fingers II–IV bearing dilated pads, discs broader than long; 8) fingers lacking lateral fringes; 9) forearm lacking ulnar tubercles; 10) heel and outer edge of tarsus bearing row of small subconical tubercles; 11) two metatarsal tubercles, inner oval, 5–6 times

size of round outer; 0–4 supernumerary plantar tubercles; 12) toes lack lateral fringes and webbing; toe pads as large as those of outer fingers; 13) dorsum gray to dull orange with dark brown to black-edged hour-glass mark on back enclosing pale gray area; flanks gray with darker slanted bars; venter cream spotted or reticulated with brown; limbs yellow-brown with darker bars; posterior thigh strongly barred; 14) adults moderate sized, males 22.9–30.3 (\bar{x} = 26.4, N = 25) mm, females 31.9–38.9 (\bar{x} = 35.9, N = 14) mm SVL.

In life, *E. chloronotus* is readily recognized because the area between the paravertebral stripes is bright (young) to dull (old) green. Most comparable-sized *Eleutherodactylus* in upper montane cloud forests have cranial crests and lateral fringes on the digits; none has so strongly concave canthus rostralis as *E. chloronotus*.

Description.—see Lynch (1970b).

Color in life.—Middorsal area bright metallic green or olive-green to orange-brown or bronze with dark brown to black dorsolateral ridges. Laterally green, tan, gray, or cream usually with brown diagonal marks. Brown or dark green bars usually evident on hind limbs. Venter creamy yellow to yellowish tan with (usually) or without brown flecks or marbling, or gray with or without cream to bluish-white flecks. Iris bronze, with a coppery tint in some individuals.

Distribution and ecology.—*Eleutherodactylus chloronotus* occurs in subpáramo and upper humid montane forest (2285–3350 m) along the eastern front of the Andes from southern Colombia (Nariño and Putumayo) southward to the Pastaza depression. By day the frogs are found beneath stones and logs, whereas at night they are active on the ground and perch on herbs and low bushes. Several were observed moving about by day after rain.

Reproduction may be seasonal. Lynch (1970b) reported egg clutches found in March at the type-locality. A newly hatched frog was found at the type-

locality in mid-July 1977 but no egg masses were found.

Remarks.—The body size of adult females reported by Lynch (1970b) is in error; he included juvenile and young females in his sample. Females having large eggs or convoluted oviducts are at least 31 mm in SVL.

Aside from being a member of the *unistrigatus* group (now containing more than 100 species), the relationships of *E. chloronotus* remain obscure. *Eleutherodactylus chloronotus* appears to be related to *E. incanus* found at lower elevations and, to a lesser degree, to *E. calcaratus* and *E. crucifer* (Pacific versant). *Eleutherodactylus cryptomelas* from the Amazonian slopes of southern Ecuador likewise appears to be related to *E. chloronotus*. Lynch's (1970b) suggestion of a close relationship between *E. chloronotus*, *E. devillei*, and *E. surdus* is untenable.

Eleutherodactylus colodactylus Lynch

Eleutherodactylus colodactylus Lynch, 1979, Misc. Publ. Mus. Nat. Hist. Univ. Kansas 66:15 [*Holotype*.—KU 142151, Abra de Zamora, 13.5 km E Loja, Provincia Loja, Ecuador, 2800 m].

Eleutherodactylus colodactylus occurs in cloud forest and subpáramo at elevations of 2200 to 2850 m on the Amazonian slopes of the Andes in southern Ecuador and on the crest and Pacific versant of the Cordillera between Canchaque and Huancabamba, Departamento de Piurá, Perú, at elevations of 2745 to 3100 m (Lynch, 1979a).

Eleutherodactylus condor new species

Fig. 2C

Holotype.—KU 146992, juvenile female, taken at Río Piuntza, Cordillera del Condor, Provincia Morona-Santiago, Ecuador, 1830 m, on 4 January 1972 by Bruce MacBryde and John E. Simmons.

Paratypes.—KU 146991, 146993–147033, collected at type-locality 3–6 Jan. 1972.

Diagnosis.—1) skin of dorsum sha-

greened with indistinct dorsolateral folds, that of venter smooth; 2) tympanum distinct, its length $\frac{1}{2}$ eye length; 3) snout subacuminate in dorsal view, rounded in lateral profile, canthus rostralis sharp; 4) upper eyelid narrower than (to equal) IOD, not bearing pungent warts; low cranial crests palpable in large females; 5) vomerine odontophores prominent, triangular in outline; 6) males with vocal slits, subgular vocal sac, non-spinuous nuptial pads on thumbs; 7) first finger longer than second; pads of outer fingers large, those of inner fingers narrow; discs broader than long; 8) fingers lacking lateral fringes or keels; 9) no ulnar tubercles except small antibrachial tubercle; 10) no tubercles on heel or tarsus; 11) two metatarsal tubercles, inner elongate, 6–8 times size of outer; 0–2 supernumerary plantar tubercles; 12) toes bearing narrow lateral fringe (keeled), not webbed; toe pads slightly smaller than those of fingers III–IV; 13) brown with darker markings—chevrons, interorbital bars, labial bars; posterior thigh brown with large cream or white spots (spots smaller than pad of any toe); venter moderately to heavily blotched with brown, darkest on throat and undersides of limbs; venter of thigh and shank cream with brown spots or brown with cream spots; 14) adults large, nine males 32.1–39.5 mm, five juvenile to young females 52.6–59.4 mm SVL. A decapitated adult female (MCZ 19630) is estimated to have been 63.2 mm SVL.

Eleutherodactylus condor is one of the largest members of the *fitzingeri* group lacking toe webbing or heavy toe fringing. Adults are probably comparable in size to *E. lymani* Barbour and Noble and *E. w-nigrum* (Boettger). *Eleutherodactylus lymani* has an inner tarsal fold; *E. w-nigrum* has smaller tympana, dark spots on the flank, and yellow posterior thighs with brown or black spots or reticulation. Except for some populations of *E. w-nigrum*, neither species has spotted throat and venter as does *E. condor*. *Eleutherodactylus con-*

dor is superficially similar (in preservative) to the Amazonian slope populations of the smaller *E. peruvianus* (adult females 38.6–46.4 mm SVL) but has less intense brown markings on the throat and chest and a narrower head.

Description.—Head as wide as or wider than body, wider than long; head width 37.0–40.2 (\bar{x} = 38.4, N = 14) percent SVL; nostrils weakly protuberant, directed laterally; snout long, E–N 85.7–109.5 (\bar{x} = 100.0, N = 9) percent eye length in males, 102.8–127.6 (\bar{x} = 114.5, N = 5) in females; loreal region weakly concave, sloping abruptly to lips; lips not flared; cranial crests not present but edges of frontoparietals slightly elevated in large females (albeit immature); upper eyelid lacking tubercles, its width 64.3–105.1 (\bar{x} = 90.7, N = 13) percent IOD; tympanum directed laterally with slight dorsal and posterior vectors, prominent, higher than long, slanted anteriorly, posterodorsal edge obscured by well-defined supratympanic fold; tympanum length 43.2–60.0 (\bar{x} = 51.2, N = 14) percent eye length; postriatal tubercles small, subconical; choanae longer than wide, relatively small, not concealed by palatal shelf of maxillary arch; vomerine odontophores median and posterior to choanae, triangular in outline, elevated, separated by distance equal $\frac{1}{2}$ choanal width, each 1.5 times size of a choana, bearing 7–9 teeth in approximately transverse row.

Skin of dorsal surfaces shagreened; ill-defined dorsolateral folds extend from posterolateral corner of eyelid to above groin; discoidal folds evident, areolation below and posterodorsal to anus poorly defined; anal opening not extended; palmar tubercle bifid, larger than oval thenar tubercle; supernumerary palmar tubercles not pungent; subarticular tubercles round, subconical; fingers lacking lateral fringes or keels; pads of fingers III–IV large, those of I–II weakly dilated; discs of former broader than long, round apically; thumb longer than second finger.

Heel and tarsus lacking tubercles or

folds; inner metatarsal tubercle weakly compressed, its length 2.5 times width; outer metatarsal tubercle round to elongate, scarcely evident, $\frac{1}{2}$ or less size of inner; 0–2 supernumerary plantar tubercles—if present, at base of toes III–IV; subarticular tubercles longer than wide, subconical to weakly elevated; toes bearing lateral keels, webbing insufficient to reach bases of basal subarticular tubercle (except toe V); pads slightly smaller than those of outer fingers; legs long, shank 54.9–64.2 (\bar{x} = 59.5, N = 9) percent SVL in males, 63.5–66.0 (\bar{x} = 64.1, N = 5) in females; heels of flexed legs broadly overlapping; heel of adpressed hind limb reaching beyond tip of snout.

In preservative, brown above with darker brown markings (chevrons, interorbital bar, limb bars, oblique flank bars, labial bars) edged with cream halos; canthal and supratympanic stripes prominent; posterior thigh brown with white spots (smaller than any toe pad); groin brown with few pale spots; throat gray with darker blotching, especially toward jaw and on breast; belly cream spotted with ill-defined brown spots; underside of thighs cream with brown spots, of shank brown with cream spots.

Color in life.—Dorsum usually tan (reddish brown, olive-green, or grayish green in some individuals) with darker tan or brown markings on body. Seven individuals (KU 146993, 147006–10, 147024) have pale cream, yellow, or orange dorsolateral stripes. Posterior surfaces of thighs gray or brown, with yellow flecks in four individuals (KU 147002–4, 147023). Venter mottled orange and yellow or orange or yellow and gray; in juveniles (KU 146991, 147006–10, 147033) venter gray with white flecks or mottling. Undersides of hind limbs black in KU 147019. Canthal and supratympanic stripes dark brown to black.

Measurements of holotype in mm.—SVL 55.5; shank 36.0; head width 20.7;

lead length 20.7; upper eyelid width 4.8; IOD 6.0; tympanum length 3.3; eye length 5.8; E–N 7.4. The oviducts of the holotype are thin, non-convoluted tubes.

Etymology.—A noun in apposition in allusion to the Cordillera del Condor and the large size of species.

Distribution and ecology.—This species is definitely known only from the type locality in cloud forest near the headwaters of the Río Piuntza on the western slopes of the Cordillera del Condor, an isolated range separated from the main Andean Cordillera by the valley of the Río Zamora. Eight adults were perched on low vegetation at night; juveniles and the rest of the adults were on the forest floor by day. Three specimens (MCZ 19629–30, 19632) bear imprecise locality data: “Pastaza River, Canelos to Marañón.” If these frogs actually were collected between Canelos and the Río Marañón, the species occurs in the lowlands of eastern Ecuador.

Remarks.—Sexual dimorphism in body size in most species of *Eleutherodactylus* is on the order of females being 140–150 percent the size of males (Crump, 1974; Lynch, 1976b, 1979a). If this relationship is true for *E. condor* (\bar{x} size of males 36.5), females should be 50–55 mm (mean). The largest females available are 57.3, 59.2, and 59.4 mm SVL and have slight convolutions of the oviduct and small eggs; presumably adult females are between 60 and 70 mm SVL (MCZ 19630 is estimated to have been 63.2 mm and is an adult female).

Eleutherodactylus condor is one of two species of the *fitzingeri* group found at moderate to intermediate elevations on the Amazonian slopes in Ecuador. *Eleutherodactylus peruvianus* has been taken at several localities including on the slopes of Volcán Sumaco but no specimens of *E. condor* have been found on that semi-isolated mountain; *E. condor* may be restricted to the Cordillera del Condor.

Eleutherodactylus cornutus

(Jiménez de la Espada)

Fig. 2D

- Limnophys cornutus* Jiménez de la Espada, 1870, *Jorn. Sci. Math. Lisbon*, 3:60 [*Holotype*.—evidently lost, taken at San Jose de Moti, Provincia Napo, Ecuador].
- Limnophys napacus* Jiménez de la Espada, 1870, *Jorn. Sci. Math. Lisbon*, 3:60 [*Holotype*.—evidently lost, taken at San Jose de Moti, Provincia Napo, Ecuador].
- Strabomantis cornutus*: Jiménez de la Espada, 1872, *Anales Soc. Español. Hist. Nat.* 1:85.
- Hylodes cornutus*: Boulenger, 1882, *Cat. Batrachia Salientia*. . . British Museum: 220.
- Ctenocranius cornutus*: Melin, 1941; *Medd. Göteborgs Mus. Zool., Avdel.* 88:49.
- Lithodytes cornutus* (part): Andersson, 1945, *Arkiv för Zoologi*, 37A(2):45.
- Eleutherodactylus cornutus cornutus* (part): Rivero, 1961, *Bull. Mus. Comp. Zoology*, 126:55.
- Eleutherodactylus cornutus*: Gorham, 1966, *Das Tierreich* (85):66; Lynch, 1975, *Occas. Pap. Mus. Nat. Hist. Univ. Kansas* (38): 28-31.

Diagnosis.—1) skin of dorsum coarsely tuberculate, bearing H-shaped folds in center of back, that of venter smooth; 2) tympanum prominent, its length $\frac{2}{3}$ eye length; 3) snout round in dorsal view, truncate in lateral profile; canthus rostralis sharp; 4) upper eyelid bearing elongate conical tubercle; heavy cranial crests ending in bosses posteromedial to eyes; 5) vomerine odontophores arch-like, extending laterally to outer edge of choanae; 6) males lacking vocal sac and slits, lacking nuptial pads; 7) first finger longer than second; pads small, discs as long as wide; 8) fingers bearing thin lateral fringes; 9) ulnar tubercles prominent; 10) row of conical tubercles on heel and outer edge of tarsus; inner tarsal fold present; 11) two metatarsal tubercles, inner elongate, outer prominent, not elevated, $\frac{2}{3}$ size of inner; supernumerary plantar tubercles minute, few in number; 12) toes bearing lateral fringes, not webbed; toe pads slightly larger than those of outer fingers; 13) brown above with dark brown facial markings; limb bars narrow; venter cream, heavily reticulated with brown; posterior thighs black with silvery or

golden flecks; 14) adults large, two males 35.5–43.0 mm, one young female 54.0 mm SVL.

Eleutherodactylus cornutus is most closely related to *E. biporcatus* (Peters) and *E. cerastes* Lynch, neither of which have an inner tarsal fold. Both *E. cerastes* and *E. cornutus* have elongate tubercles on the upper eyelid. Lynch (1975a) included these three and *E. bufoniformis* (Boulenger) and *E. neceurus* Lynch in the *biporcatus* group. All are very different from most *Eleutherodactylus* in having broad heads (head width of *cornutus* 48.8–56.4 percent SVL).

Description.—See Lynch (1975a).

Color in life.—Dorsum dull brown (reddish or olive tint in some) with or without darker brown or black markings; posterior surfaces of thighs black with minute cream, white, or bluish white flecks; throat brown or reddish brown with cream flecks; rest of venter dull creamy gray to bluish white with brown mottling; feet orange-tan in one individual; iris dull bronze to brown; tongue orange or yellow.

Distribution and ecology.—This large terrestrial species inhabits cloud forests at elevations of 1150–1800 m along the Andean front from southern Colombia (Putumayo) southward to the Cordillera Cutucú in southern Ecuador. One individual was on the forest floor by day; all others were found at night on the ground; some were on stream banks.

Eleutherodactylus cremnobates

new species

Fig. 2E

Holotype.—KU 166036, an adult female, taken 2 km SSW Río Reventador (Quito-Lago Agrio road), Provincia Napo, Ecuador, 1490 m, on 6 October 1974 by William E. Duellman.

Paratypes.—KU 166037–56, topotypes collected 19–20 March and 6 October 1974 by W. E. Duellman, A. H. Savitsky, and L. Trueb.

Diagnosis.—1) skin of dorsum finely

tuberculate, bearing short ridges and folds, that of venter finely areolate posteriorly, smooth anteriorly; 2) tympanum distinct, its length $\frac{1}{2}$ – $\frac{2}{3}$ that of eye; 3) snout subacuminate in dorsal view, rounded in lateral profile; canthus rostralis rounded; 4) upper eyelid as broad as IOD, not bearing pungent warts; cranial crests absent, although interorbital space furrowed; 5) vomerine odontophores prominent, triangular in outline; 6) males lacking vocal sac and slits; no nuptial pad in males; 7) first finger shorter than second; fingers II–IV bearing large pads; discs broader than long; 8) fingers bearing lateral fringes; 9) ulnar tubercles not distinct; 10) heel and outer edge of tarsus bearing non-conical tubercles, low ridge on distal one-half of inner tarsus; 11) two metatarsal tubercles, inner pungent, elongate, 4–6 times size of outer; numerous small supernumerary plantar tubercles; 12) toes bearing lateral fringes, not webbed; pads of toes as large as those of fingers; 13) brown above with darker marbling; posterior thigh dark brown, flecked with cream; venter pale gray to cream with brown chevron across chest separating yellowish throat with sparse brown spotting from cream belly heavily spotted with brown; 14) adults moderately large, seven males 28.4–32.5 mm, eight females 41.6–51.7 (\bar{x} = 46.2) mm SVL.

Eletherodactylus cremnobates is similar to *E. crenunguis* Lynch, *E. latidiscus* (Boulenger), and *E. rubicundus* (Jiménez de la Espada) in that all have large digital pads on long slender digits, sloping loreal regions, and weakly to strongly flared lips. *Eletherodactylus cremnobates* differs from all of these in having apically round digital pads. Both *E. cremnobates* and *E. latidiscus* have a thumb that is slightly shorter than the second finger (first slightly longer than second in *E. crenunguis* and *E. rubicundus*).

Description.—Head as broad as or broader than body, broader than long; head width 36.7–41.7 (\bar{x} = 39.8, N = 26) percent SVL; snout elongate; nos-

trils protuberant, directed laterally; E–N 80.5–93.3 (\bar{x} = 88.2, N = 7) percent eye length in males, 87.8–103.8 (\bar{x} = 95.0, N = 19) percent in females; loreal region weakly concave, sloping gradually to lips; lips weakly flared; interorbital space flat, cranial crests absent, although edges of frontoparietals higher than center toward anterior end of frontoparietals and nasals dip toward midline; upper eyelid width 91.3–124.1 (\bar{x} = 105.5, N = 26) percent IOD; temporal region not swollen; tympanic region not vertical; tympanum distinct, much smaller than pad of finger II, III, or IV; tympanum length 17.1–25.0 (\bar{x} = 21.7, N = 7) percent eye length in males, 21.0–29.3 (\bar{x} = 25.6, N = 8) percent in adult females, and 16.7–26.5 (\bar{x} = 21.4, N = 11) percent in juvenile females (latter not different from males, but different from adult females); supratympanic fold thickened, concealing upper edge of tympanic annulus; choanae relatively small, three-cornered, each smaller than an odontophore; vomerine odontophores median and posterior to choanae, separated medially by distance equal to choanal breadth, bearing teeth in a transverse row; tongue longer than wide, notched posteriorly, the posterior $\frac{2}{5}$ not adherent to floor of mouth.

Skin of dorsum finely tuberculate and bearing short ridges and folds; skin of head likewise textured, that of upper eyelid bearing slightly larger tubercles (none elongate); postrictal tubercles subconical; anal opening not modified; flanks bearing flattened tubercles, most obvious anteriorly; skin of venter finely areolate posteriorly, that over most of venter and on throat smooth; skin of thighs ventral and ventrolateral to vent coarsely areolate; discoidal folds prominent; ulnar tubercles very inconspicuous, poorly defined; palmar tubercle bifid, slightly larger than oval thenar tubercle; supernumerary palmar tubercles small, numerous, subarticular tubercles round to longer than wide, pungent, non-conical; all digits bearing discs, broader than long and apically rounded, on pads;

pads of fingers II–IV at least twice width of digit below pad, that on thumb only slightly wider than digit; pads rounded apically; fingers long and slender, thumb shorter than second finger (when adpressed, tip of I reaches proximal edge of disc of II).

One non-conical tubercle on heel, 1–3 equal sized tubercles along outer edge of tarsus; inner edge of tarsus bearing a low ridge for the distal one-half; inner metatarsal tubercle non-compressed, pungent, its length 2.5 times its width, 4–6 times size of oval outer; supernumerary plantar tubercles small, non-pungent, numerous; subarticular tubercles slightly longer than wide, pungent, non-conical; toes bearing prominent lateral fringes, which coalesce basally producing very slight webs; toes bearing broad pads and discs (broader than long, apically rounded), pads of toes III–V as large as those of outer fingers, those of toes I–II as large as that of finger II; hind limbs of moderate length; heel of adpressed leg reaches anterior to eye (between eye and nostril); when legs are flexed and held at right angles to sagittal plane, heels overlap; shank 53.1–56.8 (\bar{x} = 55.2, N = 7) percent SVL in males, 54.8–57.9 (\bar{x} = 56.6, N = 11) percent in juvenile females, and 51.3–57.2 (\bar{x} = 53.7, N = 8) in adult females.

Brown on all upper surfaces with darker brown marbling; some ridges (especially on occiput) high-lighted with pale brown; flanks suffused with gray and marbled with black; face pale brown below eye, labial bars darker brown; canthal-supratympanic stripe dark brown or black, narrow; limb bars diffuse, weakly oblique, as wide as interspaces; posterior thigh dark brown, spotted with cream (spots small); anterior surface of thigh heavily reticulated with dark brown to dark brown with cream flecks and reticulations; underside of shank heavily marbled with dark brown; venter pale gray to cream, usually heavily reticulated or spotted with brown; throat dirty yellow with sparse brown

spotting, finely stippled with brown; a diffuse to prominent brown line extending from just anterior to forearm insertion posteromedially to area above sternum where it may or may not meet its counterpart; this "line" divides the ventral surface into a yellowish forepart with sparse flecking, and a cream to gray hind part, usually heavily spotted or marbled with brown.

Color in life.—Dorsum olive-brown to dark brown with tips of some tubercles and ridges olive-tan or orange in some individuals. Hind limbs dark brown to black with creamy-tan transverse bars. Venter pink, rosy brown, to dull yellow with brown or black flecks or mottling. Iris reddish copper or coppery brown. Some individuals from the Río Salado have a yellow spot at the base of the thigh and in the groin. Venter in a juvenile creamy gray with brown marbling.

Measurements of holotype in mm.—SVL 51.7; shank 27.0; head width 20.6; head length 18.7; upper eyelid width 4.9; IOD 4.6; tympanum length 1.6; eye length 6.1; E–N 6.2. The holotype is a spent adult female having extensively convoluted oviducts.

Etymology.—Greek (*kremnos*, a cliff) and (*batēs*, one that haunts) in reference to microhabitat selection by the frog.

Distribution and ecology.—This species is known from three localities between 1410 and 1700 m on the eastern face of the Cordillera Oriental drained by the Río Coca. All individuals were found at night at various times of the year (March, April, July, October, December). Three of the frogs were perched on branches or logs over small streams in cloud forest. Seven were on leaves of herbs along small streams, and 25 were on moss, ferns, or small herbs on cliffs over streams. Two adult females are spent (KU 166036, taken in October, and KU 166044, taken in March).

Remarks.—If *E. latidiscus* is the closest relative of *E. cremnobates*, the relationship is not extremely close. Many

minor structural differences are evident between the two but they are the only moderate-sized species of the *unistri-gatus* group having large pads on slender digits, flared lips, obtuse canthi rostrali, large eyes, low cranial crests, and small tympana. In each, males lack vocal sacs and slits. *Eleutherodactylus cruentus* (Peters) may be allied but is judged less closely related to *E. cremnobates* and *E. latidiscus* than either is to one another.

Eleutherodactylus croceinguinis Lynch

Eleutherodactylus croceinguinis Lynch, 1968, Journ. Herpetol. 2:133 [Holotype.—KU 110789, Santa Cecilia, Provincia Napo, Ecuador, 340 m].

Diagnosis.—1) skin of dorsum tuberculate, that of venter coarsely areolate; 2) tympanum concealed beneath skin; 3) snout subacuminate in dorsal view, round in lateral profile; canthus rostralis sharp, weakly concave; 4) upper eyelid slightly broader than IOD; no cranial crests; 5) vomerine odontophores oval in outline; 6) males lack vocal sac and slits, no nuptial pads; 7) first finger shorter than second; pads bearing discs (broader than long), pads largest on fingers III–IV; 8) fingers lacking lateral fringes; 9) ulnar tubercles evident, small; 10) tarsus bearing row of conical tubercles along outer edge, no tubercles or fold on inner edge; small tubercle on heel; 11) two metatarsal tubercles, inner elongate, 3–4 times size of rounded outer; no supernumerary plantar tubercles; 12) toes lacking lateral fringes and webbing; toe pads slightly smaller than those of fingers; 13) dorsum and venter brown, former flecked with white and bearing darker brown markings, latter heavily flecked with cream; limb bars narrow; posterior surfaces of thighs brown; a pale spot on anterior edge of thigh (in groin), another on adjacent flank (pale spots yellow to orange in life); 14) adults small, males 12.8–18.2 (\bar{x} = 14.6, N = 14) mm, females 18.0–21.9 (\bar{x} = 19.8, N = 19) mm SVL.

Eleutherodactylus croceinguinis is mostly closely related to *E. carvalhoi* Lutz and *E. martiae* Lynch. *Eleutherodactylus martiae* lacks pale spots in the groin, vomerine odontophores are usually not apparent, and exhibits pronounced pattern polymorphism. *Eleutherodactylus carvalhoi* is more similar (it has a single yellow spot in the groin) and is allopatric.

Description.—See Lynch (1968a).

Color in life.—Dorsum yellow-brown to brown, spotted with dark brown and flecked with white or yellow; flanks brown to black, blotched with darker brown and flecked with white or yellow; venter brown (gray to black) with cream flecks; limb bars and anal triangle dark brown on paler brown ground color; spots in groin yellow to reddish-orange; iris gray, finely reticulated with black.

Distribution and ecology.—This species occurs in lowland rainforests in Ecuador and adjacent Colombia but invades low cloud forests at the base of the Pastaza Trench. In lowlands as well as cloud forests, *E. croceinguinis* is nocturnal and is found on low vegetation (0.5–1.5 m above ground) in dense forests. *Eleutherodactylus croceinguinis* from low cloud forests are no larger than specimens from the lowlands (in contrast to *E. lacrimosus*, *E. lanthanites*, *E. nigrovittatus*, and *E. peruvianus*) and are as abundant in cloud forests as in the lowlands (in contrast to *E. ockendeni*).

Eleutherodactylus cryptomelas Lynch

Eleutherodactylus cryptomelas Lynch, 1979, Misc. Publ. Mus. Nat. Hist. Univ. Kansas 66:21 [Holotype.—KU 141992, Abra de Zamora, 15 km E Loja, Provincia Zamora-Chinchipec, Ecuador, 2710 m].

This species occurs in subpáramo and cloud forests on the eastern Andean cordillera in southern Ecuador at elevations of 2470 to 3100 m (Lynch, 1979a).

Eleutherodactylus devillei (Boulenger)

Fig. 2F

Hylodes DeVillei Boulenger 1880, Bull. Soc. Zool. France 5:47 [Holotype.—MRHN 1009, adult female taken in the "Andes of Ecuador," by Émile de Ville in 1874 or 1875].

Eleutherodactylus devillei Peters, 1955, Rev. Ecuat. Ent. Par. 2:351; Lynch, 1970, Journ. Herpetol. 3:136-38.

Diagnosis.—1) skin of dorsum smooth with prominent dorsolateral folds, that of venter areolate; 2) tympanum prominent, its length $\frac{1}{2}$ – $\frac{1}{2}$ eye length; 3) snout subacuminate in dorsal view, rounded in lateral profile; canthus rostralis sharp; 4) IOD broader than upper eyelid; upper eyelid lacking tubercles; cranial crests present, low; 5) vomerine odontophores prominent, oblique; 6) males lack vocal sac and slits, no nuptial pads; 7) first finger shorter than second; pads bearing discs (broader than long), pads large on fingers II–IV; 8) fingers bearing narrow lateral fringes; 9) forearm bearing ill-defined ulnar tubercles; 10) inner tarsal fold present, no tubercles on heel or tarsus; 11) two metatarsal tubercles, inner elongate, 3–4 times size of oval outer; no supernumerary plantar tubercles; 12) toes bearing narrow lateral fringes, not webbed; toe pads slightly smaller than those of fingers; 13) dorsum brown with black or dark brown chevrons and flecks; limb bars narrow; posterior surfaces of thighs yellow-brown with brown reticulations; venter cream with brown reticulation; 14) adults moderate-sized, males 19.6–31.6 (\bar{x} = 26.8, N = 26) mm, females 34.7–44.7 (\bar{x} = 39.0, N = 26) mm SVL.

Eleutherodactylus devillei is most closely related to a series of species now called *E. vertebralis* (Boulenger) and less closely related to *E. buckleyi* (Boulenger), *E. cryophilus* Lynch, and *E. curtipes* (Boulenger). *Eleutherodactylus devillei* differs from *E. cryophilus* and *E. curtipes* in having visible tympana and large digital pads as well as in coloration (neither has reticulation on the venter). The constellation of frogs now

called *E. vertebralis* all have numerous supernumerary plantar tubercles and less prominent cranial crests. *Eleutherodactylus buckleyi* lacks an inner tarsal fold and never has a pattern consisting of thin limb bars and dorsal chevrons but frequently has a marbled or reticulate venter.

Description.—See Lynch (1970b).

Color in life.—Dorsum pale brown (bronze or reddish tint common) with dark brown to black markings. Flanks pale gray with dark mottling, pinkish cast in some. Throat and anterior belly dull yellowish white, becoming pale gray posteriorly, with dark brown to black mottling. Iris coppery bronze.

Distribution and ecology.—This species occurs in upper montane forests and clearings on the eastern slopes of the Andes in Provincia Napo, Ecuador. With the exception of a specimen from Santa Barbara, and one from "top of Sumaco," all specimens are from the valley of the Río Papallacta between 2350 and 3155 m. A record (USNM) from Borja (1710 m) needs to be verified. This frog is found beneath rocks and logs by day and on low vegetation at night.

Remarks.—Lynch (1970b) reported only females in a sample of 16 specimens and speculated that the absence of males might be a product of collection bias. We have seen more than 100 specimens and find no distortion from a 50:50 sex ratio.

Lynch (1970b) suggested that *E. devillei* was [closely] related to *E. surdus* (Boulenger). The failure to associate *E. devillei* with *E. buckleyi* or *E. vertebralis* was a result of not having specimens of *buckleyi* or *vertebralis* available (those Lynch thought to be *buckleyi* are specimens of *E. curtipes*). The purported relationship of *E. chloronotus* and *E. devillei* also represents a premature association. The relationships of *E. chloronotus* are obscure (see species account above) but are certainly not with *E. devillei*. No hint of the distinctive concave canthus rostralis of *E. chlo-*

ronotus is evident in *E. buckleyi*, *E. cryophilus*, *E. curtipes*, *E. devillei*, or *E. vertebralis*.

Eleutherodactylus dolops new species

Fig. 2G

Holotype.—KU 143505, an adult female, taken at Salto de Agua, 2.5 km NNE Río Reventador, Provincia Napo, Ecuador, 1660 m, on 25 October 1971 by William E. Duellman.

Paratypes.—KU 143504, Río Azuela, Provincia Napo, Ecuador, 1740 m; KU 165866–68, 2 km SSW Río Reventador, Provincia Napo, Ecuador, 1490 m; USNM GOV 8901, Loreto, Provincia Napo, Ecuador; USNM GOV 9332–33, Río Villano, Provincia Pastaza, Ecuador; KU 168811, 10.3 km W El Pepino, Departamento Putumayo, Colombia, 1440 m.

Diagnosis.—1) skin of dorsum pustulate, no dorsolateral folds, that of venter smooth; 2) tympanum distinct, its length $\frac{3}{4}$ – $\frac{1}{2}$ eye length; 3) snout subacuminate in dorsal view, round in lateral profile; canthus rostralis moderately sharp; 4) upper eyelid broader than IOD, not bearing pungent warts; no cranial crests; 5) vomerine odontophores prominent, triangular in outline; 6) males with vocal slits, subgular vocal sac; 7) first finger longer than second; discs as long as broad; pads narrow; 8) no lateral fringes; 9) no ulnar tubercles; 10) no tubercles on heel or tarsus; 11) two metatarsal tubercles, inner elongate, 4–8 times size of outer; no supernumerary plantar tubercles; 12) toes lacking lateral fringes and webbing; toe pads as small as those of fingers; 13) brown with darker blotches; posterior thigh brown with cream flecks; venter dirty white, reticulated with brown; 14) adults large, two males 35.8–40.3 mm, three females 56.6–57.6 mm SVL.

Eleutherodactylus dolops is most similar to and apparently related to *E. cruralis* (Boulenger), *E. discoidalis* (Peracca), *E. elassodiscus* Lynch, *E. granulatus* (Boulenger), *E. mantipus*

(Boulenger), and *E. nigrovittatus* Andersson, but *E. dolops* is considerably larger than any of these (males 21.1–29.2 mm, females 24.0–36.9 mm SVL) and has much smaller outer metatarsal tubercles (at least one-half as large as inner metatarsal tubercle in the other six species).

Description.—Head as broad as body, wider than long; head width 40.2–42.0 (\bar{x} = 41.3, N = 8) percent SVL; snout subacuminate in dorsal view, rounded in lateral profile, short, E–N 71.4–87.0 (\bar{x} = 78.1, N = 8) percent eye length; loreal region weakly concave, sloping abruptly to lips; lips not flared; nostrils lateral, weakly protuberant or not, much closer to tip of snout than to eye; upper eyelid width 100.1–152.2 (\bar{x} = 122.3, N = 8) percent IOD; no cranial crests; tympanum prominent, round in males, higher than long in females, its length 32.0–51.8 (\bar{x} = 39.5, N = 8) percent eye length; supratympanic fold heavy, concealing upper edge of tympanum, not reaching insertion of arm; postriatal tubercles forming ridge anteroventral to terminis of supratympanic fold; upper eyelid and, to lesser extent, top of head bearing numerous pustules, none enlarged; tongue relatively small, round to slightly longer than wide, its posterior edge bearing shallow notch, posterior one-sixth not adherent to floor of mouth; choanae round to triangular in outline, much smaller than a vomerine dentigerous process, contained within mesial borders of jaw; vomerine odontophores wider than long, triangular in outline, posteromedial to choanae, separated by $\frac{1}{2}$ width of an odontophore width (1.5 choanal widths), bearing a transverse row of 8–13 moderate-sized teeth along posterior border.

Skin of dorsum pustulate with short ridges along upper flanks; flanks areolate; upper surface of limbs finely pustulose; skin below vent areolate; discoidal folds prominent; palmar tubercle bifid, as large as oval thenar tubercle; supernumerary palmar tubercles low, flat, at base of each digit; subarticular tubercles

elongate, subconical, simple; fingers long, slender, thumb longer than second finger; fingers lacking lateral fringes, but feebly keeled laterally; fingers bearing weakly dilated pads, all pads bearing discs, discs as wide as long or longer than wide; pads and discs of fingers I and II pointed, those of III and IV rounded apically.

Heel and tarsus lacking tubercles or folds; two metatarsal tubercles, inner metatarsal tubercle 2.5 times as long as wide, not elevated or compressed, 7–8 times size of round (subconical in KU 143504) outer metatarsal tubercle; in KU 143505 the outer metatarsal tubercle is low and flat, $\frac{1}{4}$ – $\frac{1}{2}$ size of inner; no supernumerary plantar tubercles; subarticular tubercles longer than wide, subconical, simple; no lateral fringes on toes, edges weakly keeled; toes lacking webbing; all toes with pads and discs, tips rounded or acutely rounded, discs longer than wide; hind legs long, shank 59.2–69.4 (\bar{x} = 63.6, N = 8) percent SVL; heel of adpressed hind limb extends beyond snout tip; heels of flexed hind legs overlap.

In preservative, brown above with darker brown markings (labial bars, canthal and supratympanic stripes, interorbital triangle, spots on back and flanks, limb bars); groin and posterior thigh surfaces brown with cream flecks; venter cream heavily reticulated with brown; throat, chest, and underside of limbs brown with cream flecks.

Color in life.—Dorsum dull tan to brown with darker brown to black markings; posterior surfaces of thighs orange-brown, reddish brown, or dark brown with cream or pale yellow flecks. Venter creamy yellow to pinkish tan with brown mottling or dark brown to black with bluish white flecks. Iris dull brown with grayish or reddish tint.

Measurements of holotype in mm.—SVL 57.6; shank 34.1; head width 24.2; head length 22.0; upper eyelid width 7.0; IOD 4.6; tympanum length 2.8; eye length 7.7; E–N 5.5. Each vomerine odontophore has 10 teeth. The holotype

is a gravid female with heavily convoluted oviducts and large (4.0–4.5 mm in diameter), yellow ovarian eggs.

Etymology.—Greek, meaning one hiding in ambush, in allusion to the frogs being found behind waterfalls.

Distribution and ecology.—This species is definitely known from elevations of 1440 to 1950 m on the eastern face of the Andes in Departamento Putumayo, Colombia, and Provincia Napo, Ecuador. Three specimens in the USNM were received from Gustavo Orces-V. and collected by the Olalla brothers, supposedly at Loreto (550 m) and Río Villano (< 500 m). These localities are questioned until additional material is acquired from the lowlands.

Eleutherodactylus dolops inhabits streams in cool cloud forest. Three were sitting on boulders in streams at night, and one was perched on a low bush adjacent to a stream at night. By day, two were under rocks at the edge of a stream, one was under a rock in the splash zone of a waterfall, and one was in a crevice under moss behind a waterfall.

Eleutherodactylus elassodiscus Lynch

Fig. 2H

Eleutherodactylus elassodiscus Lynch, 1973, Copeia 1978(2):222 [*Holotype.*—USNM 167668, adult female from Cuyujúa, Provincia Napo, Ecuador, 2380 m].

Diagnosis.—1) skin of dorsum smooth to feebly pustulate, no dorsolateral folds, that of venter smooth; 2) tympanum prominent, its length $\frac{3}{4}$ – $\frac{1}{2}$ eye length; 3) snout subacuminate in dorsal view, sloping in lateral profile, canthus rostralis poorly to moderately well-defined; 4) upper eyelid narrower than (to equal) IOD; no cranial crests; small pustules on upper eyelid; 5) vomerine odontophores prominent, broad, extending laterally to choanae; 6) males lacking vocal sac and slits, no nuptial pad; 7) first finger longer than second, all bearing narrow digital pads, rounded apically; discs as long as wide or longer

than wide; 8) fingers lacking lateral fringes or keels; 9) no ulnar tubercles; 10) no tubercles on heel or tarsus; 11) two metatarsal tubercles, inner oval, approximately same size as rounded outer; no supernumerary plantar tubercles; 12) toes lacking fringes or webbing; toe pads narrow, as large as those of fingers; 13) dorsum gray to brown with or without brown markings; limbs barred; posterior surface of thigh gray to brown (unicolor); venter cream with some brown mottling on throat; 14) adults moderate-sized, males 22.0–29.2 mm, females 29.7–36.9 mm SVL.

Eleutherodactylus elassodiscus is a member of the *discoidalis* group (Lynch, 1976b), which also includes *E. cruralis* (Boulenger), *E. discoidalis* (Peracca), *E. dolops* Lynch and Duellman, *E. granulatus* (Boulenger), *E. mantipus* (Boulenger), and *E. nigrovittatus* Andersson. The sloping snout of *E. elassodiscus* and *E. nigrovittatus* distinguish that pair of species from the other five species. *Eleutherodactylus nigrovittatus* has pointed digital pads, the inner metatarsal tubercle is twice as large as the outer, and males have a fleshy swelling of the upper lip and snout tip.

Description.—See Lynch (1973a).

Color in life.—Dorsum pinkish tan to grayish brown with olive-brown to dark brown markings; stripe below tympanum (postrictal) creamy orange; posterior surfaces of thighs reddish or orangish brown; venter gray to brown, with or without silvery flecks laterally; iris bronze, heavily flecked with black.

Distribution and ecology.—This terrestrial species occurs at elevations of 2300 to 2900 m in upper humid montane forest on the eastern slopes of the Andes in extreme southern Colombia (Departamento Putumayo) and northern Ecuador (Provincia Pastaza). A record from Borja, Ecuador (1710 m) needs to be verified. All specimens were found under rocks and logs by day.

Eleutherodactylus eriphus new species

Fig. 3A

Holotype.—KU 166031, an adult female, taken at the Río Jatuntinahua, 10 km SE Cuyujúa, Provincia Napo, Ecuador, 2160 m, on 21 March 1976 by Alan H. Savitsky and John E. Simmons.

Paratypes.—KU 166032–35 collected syntopically with holotype; KU 155451–55, from 12 km E Papallacta, Provincia Napo, Ecuador, collected 9 January 1974 by Ronn Altig.

Diagnosis.—1) skin of dorsum bearing many small spinules (small conical tubercles), that of venter coarsely areolate; 2) tympanum prominent, its length $\frac{1}{2}$ – $\frac{2}{3}$ that of eye; 3) snout round in dorsal and lateral profiles; canthus rostralis sharp; 4) upper eyelid as wide as IOD, bearing one pungent tubercle; no cranial crests; 5) vomerine odontophores moderately prominent, round to obliquely oval in outline; 6) males with vocal slits and subgular vocal sac; 7) first finger shorter than second, pads largest on fingers III–IV, discs broader than long; 8) fingers bearing narrow lateral fringes; 9) ulnar tubercles conical to subconical, coalescing to form ridge; 10) knee, heel, and outer edge of tarsus bearing small conical tubercles; 11) two metatarsal tubercles, inner oval, 3 times size of subconical outer; numerous supernumerary tubercles; 12) toes bearing narrow lateral fringes, not webbed; toe pads as large as those of fingers; 13) brown above with indistinct darker brown chevrons, canthal, labial, and supratympanic markings; posterior surfaces of thigh barred white and dark brown; white spots on concealed shank; venter brown with diffuse brown spots; 14) adults moderate-sized, nine males 18.1–25.2 mm, two adult females 25.8–29.0 mm SVL.

Although distinctive in having boldly barred thighs and warty skin on the dorsum, *E. eriphus* may be the Amazonian slope replacement for *E. calcarius* (Boulenger) and *E. crucifer* (Boulenger). It differs from these species in

having a straight (or weakly concave) canthus rostralis and in having boldly marked thighs. The heel tubercle of *E. calcaratus* is longer than that of *E. eriphus*. *Eleutherodactylus crucifer* has crenulate lateral fringes on the digits. *Eleutherodactylus eriphus* appears closely related to *E. nigrogriseus* and *E. spinosus*. All three have bold patterns on the posterior surfaces of the thighs (bars in *E. eriphus* and large spots in the other two species). The skin texture of *E. eriphus* is matched by *E. spinosus* Lynch from the Amazonian slopes of southern Andean Ecuador but *E. spinosus* is slightly larger, has cranial crests (albeit low), 2–3 enlarged tubercles on the upper eyelid, males lacking vocal sac and slits, and the posterior surfaces of the thigh and groin are black enclosing white spots.

Description.—Head as wide as or wider than body, wider than long; head width 34.8–40.7 ($\bar{x} = 37.6$, $N = 10$) percent SVL; snout shorter in small individuals, E–N 75.0–91.7 ($\bar{x} = 83.0$, $N = 5$) percent eye length in males, 80.0 in two juvenile females (18.9–19.6 mm SVL), 100.0–106.2 ($\bar{x} = 103.9$, $N = 3$) in young and adult females; nostrils weakly protuberant, directed dorsolaterally; canthus rostralis straight in males, concave in females; loreal region concave, sloping abruptly (small individuals) to gently (large females) to lips; lips not flared in small individuals, weakly flared in adult females; interorbital space flat (no cranial crests); upper eyelid width 84.0–122.2 ($\bar{x} = 96.8$, $N = 9$) percent IOD; one conical tubercle on upper eyelid; supratympanic fold short, evident above and behind tympanum, concealing tympanic annulus; tympanum prominent, round, separated from eye by distance equal tympanum length; tympanum length 33.3–40.0 ($\bar{x} = 36.2$, $N = 10$) percent eye length; choanae round, relatively small, not concealed by palatal shelf of maxillary arch; vomerine odontophores median and posterior to choanae, moderately elevated, round to obliquely oval, separated by distance

equal their own width in small individuals, not separated in adult females; each odontophore about size of a choana and bearing 2–3 teeth in small individuals, larger than a choana and bearing 4–6 teeth in a slanted row in adult females; tongue longer than wide, posterior border shallowly notched, posterior $\frac{1}{2}$ not adherent to floor of mouth.

Skin of dorsal surfaces bearing many small spinules, becoming sparse on flanks, no dorsolateral folds; skin of venter coarsely areolate; discoidal folds prominent, well anterior to groin; vent not extended by sheath; subanal tubercles conical; forearm bearing conical to subconical (adult females) ulnar tubercles, partially connected in ridge; palmar tubercle bifid, larger than oval thenar tubercle; numerous small supernumerary palmar tubercles; fingers bearing narrow lateral fringes; outer edge of hand and fourth finger bearing lateral fold; in small individuals (all but adult female), basal subarticular tubercles of fingers I and IV round, non-conical, subarticular tubercle on II, both on III, and distal tubercle on IV, paired; in adult females all tubercles single, distal tubercle broader than long; fingers bearing discs (broader than long) on apically rounded pads; pads of III–IV larger than those on inner fingers.

Knee, heel, and outer edge of tarsus bearing small conical tubercles; inner edge of tarsus lacking tubercles or with two small tubercles or a thin tarsal ridge; inner metatarsal tubercle 2–3 times as long as wide, not compressed, outer metatarsal tubercle round, subconical, $\frac{1}{3}$ – $\frac{1}{2}$ size of inner; numerous supernumerary plantar tubercles; toes bearing narrow lateral fringes, similar fringes along inner border of toe I and outer border of toe V and foot; all toes bearing broad discs on apically round pads; pads largest on lateral toes; heels overlap when hind legs flexed; heel of adpressed hind leg reaches to between eye and nostril; shank 52.0–59.2 ($\bar{x} = 55.3$, $N = 10$) percent SVL.

In preservative, pale to medium

brown with darker brown chevrons, canthal and supratympanic stripes, indefinite labial bars; flanks slightly darker than dorsum with white areas at base of arm and in axilla and slightly oblique white bars on posterior flank; venter brown with slightly darker spotting and marbling; inside of elbow bearing white spot; forearms bearing diffuse brown bars; thighs barred white and dark brown with pale brown stripe on top of thigh; anal triangle dark brown; concealed shank dark brown with large white spots; shank brown with indistinct darker bars.

Color in life.—Dorsum pale green with dark olive markings; flanks and hidden surfaces of limbs mottled cream and black; venter greenish white heavily suffused with black; iris reddish copper.

Measurements of holotype in mm.—SVL 29.0; shank 15.5; head width 11.7; head length 10.3; upper eyelid width 2.8; IOD 2.9; tympanum length 1.2; eye length 3.6; E-N 3.8. The holotype is a gravid female.

Etymology.—Greek, a young goat; name is used in allusion to the call of the frog (goat-like).

Distribution and ecology.—This small species is known from only two localities along the valley of the Río Papallacta on the eastern face of the Andes in Provincia Napo, Ecuador; the elevational range is 2160–2630 m. At 12 km ESE of Papallacta five individuals were found on low vegetation at night in January 1974. At the Río Jatuntinahua, a tributary of the Río Papallacta, five were on low herbs at night. Males were calling: “bleep-ee-eep.” At both localities the frogs were found in partially cleared cloud forest.

Remarks.—Five specimens (WCAB 37903, 37905, 37907–09) are purportedly from Papallacta; the specimens were purchased from a professional collector, and other material in the collection suggests that the frogs originated from lower in the valley of the Río Papallacta. The specimens are not well preserved and differ from the type-specimens in

having a more pointed snout and flattened spinules on the dorsum.

Eleutherodactylus galdi (Jiménez de la Espada)

Pristimantis galdi Jiménez de la Espada, 1870, Journ. Sci. Math. Lisboa 3:62 [Types apparently lost, originally in Museo Nacional, Madrid; type-locality, San Jose de Moti, Provincia Napo, Ecuador].

Hylodes galdi: Boulenger, 1882, Catalogue Batrachia Salientia . . . British Mus.: 219.

Hylodes festae Peracca, 1904, Boll. Mus. Zool. Anat. 19(465):28 [Holotype.—MSNT An 413, ex. 3776, adult male collected at San José de Cuchipamba, Provincia Morona-Santiago, Ecuador, 1000 m, by E. Festa].

Hylodes margaritifer Boulenger, 1912, Ann. Mag. Natur. Hist. (8)10:189 [Cotypes.—BM 1912.11.1.54–55/RR 1947.2.16.78–79, collected at El Topo, Río Pastaza, Provincia Tungurahua, Ecuador, 4200 ft., by M. G. Palmer].

Eleutherodactylus festae: Peters, 1955, Rev. Ecuat. Ent. Par. 2:348.

Eleutherodactylus margaritifer: Peters, 1955, Rev. Ecuat. Ent. Par. 2:349.

Eleutherodactylus galdi: Peters, 1955, Rev. Ecuat. Ent. Par. 2:350; Lynch, 1969, Herpetologica 25:270–72; Lynch, 1974, Occas. Pap. Mus. Nat. Hist. Univ. Kansas (31): 15–16.

Diagnosis.—1) skin of dorsum smooth or finely shagreened with scattered pustules, no dorsolateral folds, that of venter areolate and bearing much enlarged warts scattered among smaller areolations; 2) tympanum distinct, its length $\frac{1}{4}$ – $\frac{1}{2}$ eye length; 3) snout acuminate in dorsal view, truncate in lateral profile, tip somewhat swollen; canthus rostralis sharp, strongly concave; 4) IOD greater than upper eyelid width; upper eyelid bearing conical tubercle; cranial crests present, serrate in large females; otic ramus of squamosal also bearing a serrate crest in large females; 5) vomerine odontophores oblique; 6) males with vocal sac and slits, no nuptial pads; 7) first finger shorter than second; fingers II–IV bearing broad discs on large dilated pads; 8) fingers bearing ill-defined lateral fringes; 9) row of conical ulnar tubercles present; 10) row of conical tubercles along outer edge of tarsus, heel and foot; tubercles along outer edge

of shank; 11) two metatarsal tubercles, inner elongate, 5–6 times size of oval outer; no supernumerary plantar tubercles; 12) toes bearing ill-defined lateral fringes, no webbing; toe pads slightly smaller than those of outer fingers; 13) body pale cream (bright green in life) with dark brown canthal and supratympanic stripes, interorbital and limb bars, sparse spotting of dorsum; venter cream, dusted with brown; 14) adults moderate-sized, males 17.1–24.8 (\bar{x} = 21.0, N = 8) mm, females 28.1–34.0 (\bar{x} = 31.7, N = 11) mm SVL.

Eleutherodactylus inusitatus (described below) is superficially similar to *E. galdi* but lacks cranial crests and enlarged warts on the belly, has a shorter snout, and has elongate tubercles on the eyelid, heel, and elbow. We are aware of no other *Eleutherodactylus* having serrate frontoparietal and squamosal crests or having the enlarged warts on the belly.

Descriptions.—See Jiménez de la Espada (1870, 1875), Boulenger (1912), and Lynch (1969a, 1974).

Color in life.—Dorsum bright green with or without 1) white, gold, or tan flecks, 2) bronze-brown or black spots and/or transverse bars on limbs; belly white, heavily suffused with green or not, with black flecks laterally or not; other ventral surfaces green; yellow or white labial stripe and bronze canthal stripe present or not; iris green.

Distribution and ecology.—This arboreal species is widely distributed along the eastern face of the Andes in Ecuador, including Volcán Sumaco and the Cordillera del Condor. All specimens bearing elevational data are from 1000–1830 m. Records from Loreto (510 m) are questioned. Our specimens were all on vegetation (leaves of bushes 1 m above ground to a palm frond 2 m above ground) in cloud forest at night.

Eleutherodactylus gladiator Lynch

Fig. 3B

Eleutherodactylus gladiator Lynch, 1976, Her-

petologica 32:316 [*Holotype*.—KU 143516, 3.3 km ESE Cuyujúa, Provincia Napo, Ecuador, 2350 m].

Diagnosis.—1) skin of dorsum smooth with short ridges, no dorsolateral folds, that of venter arcolate; 2) tympanum prominent, its length $\frac{2}{3}$ – $\frac{1}{2}$ eye length; 3) snout acuminate in dorsal view (tip feebly pointed), round in lateral profile; canthus rostralis moderately sharp; 4) upper eyelid much narrower than IOD, lacking pungent tubercles; no cranial crests; 5) vomerine odontophores concealed, oblique; 6) males with vocal slits and subgular vocal sac; males lacking nuptial pads; 7) first finger shorter than second, discs on fingers II–IV, pads of III–IV rounded; 8) fingers lacking lateral fringes; 9) ulnar tubercles obscure; 10) small, non-conical tubercles on heel, outer edge of tarsus; ridge-like inner tarsal fold; 11) two metatarsal tubercles, inner elongate, three times size of round outer; few supernumerary plantar tubercles; 12) toes lack lateral fringes, no webbing; 13) brown above with dark brown spots; limb bars narrow, oblique; venter cream with brown flecks; colorless areas in axilla, groin, anterior and posterior surfaces of thigh (colorless areas orange in life); 14) adults small, three males 14.9–15.6 mm SVL, one immature female 15.8 mm SVL.

Eleutherodactylus gladiator was grouped with *E. leoni* Lynch and *E. pyrrhomerus* Lynch but is the most distinct of the three (Lynch, 1976a), differing in having tubercles on the heel and tarsus, less prominent tubercles on the upper eyelid and at the corner of the jaw, and comparatively larger digital pads.

Description.—See Lynch (1976a).

Color in life.—Dorsum brown to orange-tan with brown markings; flanks green to orange-tan; venter gray to yellow-gray; throat yellow; concealed thighs and groin orange-tan to orange; iris bronze to gray-brown with red-brown horizontal streak.

Distribution and ecology.—This small terrestrial species is known only from the upper Río Papallacta Valley in Provincia Napo, Ecuador, where it has been found by day under rocks and logs in cloud forest and clearings at elevations of 2350–2910 m.

Eleutherodactylus glandulosus

(Boulenger)

(Fig. 3C)

Hylodes glandulosus Boulenger, 1880, Bull. Soc. Zool. France 5:47 [*Holotype*.—IRSNB 1010, adult female taken in the “Andes of Ecuador” by Émile de Ville in 1874-75].

Eleutherodactylus glandulosus: Peters, 1955, Rev. Ecuat. Ent. Par. 2:351; Lynch, 1970, Journ. Herpetol. 3:138–39.

Diagnosis.—1) skin of dorsum weakly glandular, no dorsolateral folds, that of venter coarsely areolate; 2) tympanum prominent, its length $\frac{1}{2}$ – $\frac{1}{2}$ eye length; 3) snout round in dorsal view, truncate in lateral profile; canthus rostralis sharp, concave; 4) upper eyelid narrower than IOD, lacking tubercles; low cranial crests present; 5) vomerine odontophores low, weakly slanted or subtriangular in outline; 6) males with vocal slits and subgular vocal sac; no nuptial pads; 7) first finger shorter than second; discs broad, on broad pads, pads of II–IV large; 8) fingers bearing ill-defined lateral fringes; 9) ulnar tubercles present, small; 10) no tubercles on heel or outer edge of tarsus; low inner tarsal fold present; 11) two metatarsal tubercles, inner oval, 4 times size of round outer; numerous small supernumerary plantar tubercles; 12) toes bearing ill-defined lateral fringes, no webbing; toe pads smaller than those of fingers; 13) dorsum yellow-tan to brown with indefinite brown blotches; limbs not barred; venter pale yellow with or without sparse brown reticulation; flanks, groin, anterior and posterior thigh surfaces, concealed shank brown with large yellow spots; 14) adults moderate-sized, males 24.2–30.2 (\bar{x} = 26.6, N = 27) mm, females 31.8–41.3 (\bar{x} = 36.1, N = 20) mm SVL.

Eleutherodactylus glandulosus is not

easily confused with any other species of *Eleutherodactylus* but is most similar to *E. acerus* Lynch and Duellman, *E. leucopus* Lynch, and *E. lividus* new species, none of which have the distinctive yellow spots on the flanks and concealed limb surfaces.

Description.—See Lynch (1970b).

Color in life.—Dorsum dull tan, yellowish tan, olive-tan, or brown with yellow spots on flanks and posterior surfaces of thighs; venter dull cream to gray; iris grayish bronze.

Distribution and ecology.—This species occurs at elevations of 2105–2890 m in the upper Río Papallacta Valley on the eastern slopes of the Andes in Provincia Napo, Ecuador. A record from Borja (1710 m) is questionable. Individuals have been found under rocks and logs in cloud forest and clearings by day; at night they have been found on rocks, ground and low vegetation. Males were actively calling from low (0.3–1.5 m) vegetation during a rain on July 1977, 11 km ESE Papallacta; few males were found in the woods adjacent to the clearing.

***Eleutherodactylus ignicolor* new species**

(Fig. 3D)

Holotype.—KU 165879, a juvenile female, taken at the Río Jatuntinahua, 10 km SE Cuyujúa, Provincia Napo, Ecuador, 21 March 1975 by William E. Duellman.

Paratypes.—KU 165880, 11 km ESE Papallacta, Provincia Napo, 2660 m; KU 177296–97, 9.2 km ESE Papallacta, Provincia Napo, Ecuador, 2750 m.

Diagnosis.—1) skin of dorsum bearing low warts, especially on lower back, that of venter smooth; 2) tympanum distinct, its length $\frac{3}{4}$ – $\frac{1}{2}$ eye length; 3) snout acuminate in dorsal view, rounded in lateral profile; canthus rostralis sharp; head longer than wide; 4) upper eyelid narrower than IOD; not bearing pungent warts; no cranial crests; 5) vomerine odontophores small, oval in outline; 6) males with vocal slits, subgular vocal

sac; 7) first finger shorter than second; pads on II–IV moderate-sized; discs broader than long; 8) fingers bearing lateral keels; 9) small ulnar tubercles present; 10) no tubercles on heel; two tubercles on outer edge of tarsus; short inner tarsal fold; 11) two metatarsal tubercles, inner oval, 4–6 times size of round outer; few (3–6) supernumerary plantar tubercles; 12) toes not webbed, lateral keels indistinct; toe pads smaller than those of outer fingers; 13) brown above with dark interorbital bar, dorsal blotch, facial bars and stripes; posterior thigh brown with white spots; groin red in life; brown chevrons on throat; venter brown with white spots; 14) adults small, one male 18.0 mm, one adult female 26.4 mm SVL.

Eleutherodactylus ignicolor is most closely related to *E. prolatus* new species (see below). The two species are also closely related to *E. trachyblepharis* (Boulenger) and *E. variabilis* Lynch. These four small frogs have elongated heads (head length greater than head width), acuminate snouts, and narrow digital pads. *Eleutherodactylus ignicolor* is mostly readily distinguished in having red areas in the groin (in life) and white spots on the posterior surfaces of the thighs. *Eleutherodactylus ignicolor* and *E. prolatus* have small tubercles along the outer edge of the tarsus but *E. ignicolor* lacks tubercles on the heel.

Description.—Head as wide as body, longer than wide; head width 35.0–37.1 (\bar{x} = 36.0, N = 3) percent SVL; snout long; E–N 83.3–87.9 (\bar{x} = 84.8, N = 3) percent eye length; nostrils weakly protuberant, directed dorsolaterally, loreal region weakly concave, sloping abruptly to lips; lips not flared; upper eyelid lacking prominent tubercles, its width 77.3–100.0 (\bar{x} = 89.5, N = 3) percent IOD; interorbital space flat, no cranial crests; supratympanic fold not prominent; tympanum distinct, round in males, higher than long in females, separated from eye by less than tympanum length; tympanum length 43.3–50.0 (\bar{x} = 46.3, N = 3) percent eye length; postrictal tubercles

small, prominent; choanae relatively small, round, not concealed by palatal shelf of maxillary arch; vomerine odontophores median and posterior to choanae, smaller than a choana, separated medially by distance equal $\frac{1}{3}$ – $\frac{1}{2}$ width of an odontophore, each odontophore oval, bearing teeth in transverse row; tongue broader than long, its posterior border feebly notched, posterior one-third not adherent to floor of mouth.

Skin of dorsum smooth with low warts on posterior back, no dorsolateral folds, discoidal folds well anterior to groin; warts on flanks larger than areolations on venter; no anal sheath or tubercles; skin of head smooth; palmar tubercle bifid, much larger than oval thenar tubercle; many supernumerary palmar tubercles, slightly smaller than subarticular tubercles which are round, pungent; narrow lateral keels on fingers; pad of I round, those of II–IV broader than long, discs broader than long; pads of fingers III–IV narrower than tympanum, feebly emarginate.

No tubercles on heel; two small tubercles along outer edge of tarsus; inner edge of tarsus bearing short, low folds; inner metatarsal tubercle oval, its length twice width, 4–6 times size of rounded outer metatarsal tubercle; supernumerary plantar tubercles at bases of toes II–IV, few on plantar surface proper; subarticular tubercles round, pungent; keels on lateral margins of toes indistinct; toe pads smaller than those of outer fingers, apically rounded; heels of flexed hind legs overlap; shank 55.7–57.8 (\bar{x} = 56.5, N = 3) percent SVL.

In preservative, tan or brown above with darker brown markings (interorbital bar, canthal and supratympanic stripes, labial bars, oblique flank bars, blotches on back, oblique shank bars); anal triangle brown; posterior surface of thighs brown with white spots; throat brown with darker brown chevrons; venter brown with white spots; groin and posterior flank red.

Color in life.—Dorsum yellowish tan to brown with dark brown to black

markings, with or without orange mid-dorsal stripe; groin and proximal anterior surfaces of thighs salmon-red to dark red, with black reticulations in former; throat gray with black bars edged with cream; belly pale gray to salmon with black markings; iris dark red.

Measurements of holotype in mm.—SVL 21.1; shank 11.8; head width 7.6; head length 7.8; upper eyelid width 2.2; IOD 2.4; tympanum length 1.3; eye length 3.0; E-N 2.5. The holotype is a juvenile female with straight, non-convoluted oviducts and small ovarian eggs.

Etymology.—Latin, *ignis* (fire) and *color* (color) in reference to the flash colors in the groin.

Distribution and ecology.—An inhabitant of upper humid montane forest, this small frog is known only from the upper Río Papallacta Valley (2160–2750 m) in Provincia Napo, Ecuador. All individuals were found on bushes, a root, and bamboo at the edges of small cascading streams at night.

Eleutherodactylus incanus new species

Fig. 3E

Holotype.—KU 143465, an adult female, from a series collected at the Río Azuela, Provincia Napo, Ecuador, 1740 m, 20 October 1971 by J. T. Collins and William E. Duellman.

Paratypes.—KU 143466–83, topotypes 20–23 October 1971; KU 143457–58, 143460, 16.5 km NNE Santa Rosa, Provincia Napo, Ecuador, 1700 m.

Diagnosis.—1) Skin of dorsum bearing scattered pustules, no dorsolateral folds, that of venter coarsely areolate; 2) tympanum distinct although partially concealed, its length $\frac{1}{4}$ – $\frac{2}{5}$ eye length; 3) snout subacuminate in dorsal view, rounded in lateral profile; canthus rostralis rounded, loreal region sloping gradually to lips; 4) upper eyelid broader than IOD, especially in males, not bearing pungent warts; no cranial crests; 5) vomerine odontophores large, oblique (slanted); 6) males lacking vocal sac and slits; 7) first finger shorter than sec-

ond; fingers II–IV bearing very large pads; discs broader than long; 8) fingers bearing narrow lateral fringes; 9) forearm pustulose, ulnar tubercles present; 10) conical tubercles on knee, heel, and outer edge of tarsus; 11) two metatarsal tubercles, inner oval, 6–8 times size of outer; numerous supernumerary plantar tubercles; 12) toes bearing prominent lateral fringes, no webbing; toe pads smaller than those of outer fingers; 13) dorsum brown with darker brown markings, venter cream flecked with brown; flanks, thigh, and concealed shank spotted with glossy-white; concealed flank, thighs, and shank reddish brown with white spots; 14) adults moderate-sized, males 14.9–19.4 mm, females 23.9–30.6 mm SVL.

Eleutherodactylus incanus is a member of the *unistrigatus* group and among Ecuadorian species is distinctive in having a rounded canthus. In color, habitus, and size it resembles *E. crucifer* (Boulenger) from comparable trans-Andean sites but differs in lacking an enlarged tubercle on the upper eyelid and in lacking crenulate fringes on the digits. The head is relatively broad for a species of the *unistrigatus* group (see Lynch, 1975a).

Description.—Head broader than body in males and young females, narrower than body in adult females; head broader than long; head width 39.9–41.1 (\bar{x} = 40.5, N = 4) percent SVL in males, 41.4–45.0 (\bar{x} = 42.5, N = 9) in females; snout subacuminate in dorsal view (less so in smaller specimens), round in lateral profile; snout moderately long, E-N 75.0–82.8 (\bar{x} = 77.4, N = 4) percent eye length in males, 85.3–100.0 (\bar{x} = 92.1, N = 9) in females; nostrils weakly to prominently protuberant (more so in males), directed dorsolaterally; loreal region concave, sloping gradually to lips; lips not flared; interorbital space flat, slightly broader than upper eyelid, upper eyelid broad, its width 120.0–142.1 (\bar{x} = 130.2, N = 4) percent IOD in males, 92.6–117.7 (\bar{x} = 104.1, N = 9) in females; supratympanic

fold thick, warty, concealing upper and posterior edges of tympanic annulus; temporal regions sloping (not vertical); tympanum distinct, although partially concealed, round, its diameter 25.0–31.0 (\bar{x} = 27.8, N = 4) percent eye length in males, 29.4–40.0 (\bar{x} = 35.6, N = 9) in females; tympanum directed dorso-laterally with slight posterior vector, separated from eye by twice tympanic diameter; upper eyelid and skin near tympanum bearing small conical warts; postrictal tubercles large; choanae small, round, not concealed by palatal shelf of maxillary arch; vomerine odontophores median and posterior to choanae, elevated, oblique, separated by distance equal to one-half to full width of choanae, each larger than a choana, bearing 2–7 teeth in an oblique row; tongue round, posterior edge notched, posterior two-fifths not adherent to floor of mouth.

Skin of dorsum and flanks pustulose, pustules scattered; no dorsolateral folds; discoidal folds well antieriad to groin; anal opening not elongated by sheath; skin of forearm pustulose, but enlarged tubercles present along outer edge of arm; palmar tubercle bifid, larger than oval thenar tubercle; numerous supernumerary palmar tubercles; subarticular tubercles round, elevated; fingers bearing narrow lateral fringes; outer edge of hand bearing conical tubercles; all digits bearing broad discs on pads; pad of thumb scarcely enlarged, those of II–IV very broad, round apically.

Heel and knee bearing several conical tubercles; outer edge of tarsus bearing 2–3 conical tubercles, inner edge bearing one non-conical tubercle just proximal to inner metatarsal tubercle; inner metatarsal tubercle oval, 1.5 times as long as wide, not compressed; outer metatarsal tubercle subconical, $\frac{1}{2}$ – $\frac{2}{3}$ size of inner; plantar surface bearing tubercles along metatarsals; subarticular tubercles round, elevated, smaller than those of fingers; toes bearing prominent lateral fringes, no webs; all toes with discs (broader than long) on apically round pads; toe pads smaller

than those of fingers; heel of adpressed hind leg reaches nostril; heels of flexed hind legs overlap; shank 51.4–53.4 (\bar{x} = 52.2, N = 4) percent SVL in males, 52.9–59.4 (\bar{x} = 56.8, N = 9) in females.

In preservative, dorsum brown with darker brown interorbital bar, occipital W, chevron on sacrum (arms extended onto flank), canthal-supratympanic stripe, labial bars, limb bars; limb bars oblique on shank, narrower than interspaces; anal triangle brown; venter cream flecked with dark brown; concealed areas on flanks, thigh, shanks reddish brown (in some nearly black) with white spots; reddish areas on upper flanks and top of thighs; flanks, thigh, and concealed shank appear painted with bright enamel-white spots.

Color in life.—Dorsum green with darker green or reddish brown mottling; flanks and posterior thighs dark red with white spots; inner two fingers and inner two toes yellow; venter yellow with black spots; iris bronze with black reticulations.

Measurements of holotype in mm.—SVL 27.8; shank 15.7; head width 11.5; head length 11.3; upper eyelid 3.2; IOD 3.2; tympanum length 1.2; eye length 3.8; E–N 3.4.

Etymology.—Latin, *incanus* (hoary) in reference to white spots on the flanks and concealed limb surfaces.

Distribution and ecology.—This distinctive frog was found at two localities at 1700 and 1740 m on the eastern face of the Andes in Provincia Napo, Ecuador, in October 1971. All were in well-shaded cloud forest. One was in moss on a tree trunk by day, and 21 were on bushes or low trees at night.

Eleutherodactylus incomptus

new species

Fig. 3F

Holotype.—KU 143484, an adult male, taken 16.5 km NNE Santa Rosa, Provincia Napo, Ecuador, 1700 m, on 17 October 1971 by Joseph T. Collins.

Paratypes.—KU 143455, 143461–64,

143485–86, collected at type-locality 17–19 October 1971 by J. T. Collins and W. E. Duellman.

Diagnosis.—1) skin of dorsum bearing low flat warts, that of venter coarsely areolate; 2) tympanum distinct, its length $\frac{1}{2}$ – $\frac{2}{3}$ that of eye; 3) snout subacuminate to round in dorsal view, round in lateral profile; canthus rostralis rounded; 4) upper eyelid as wide as IOD, not bearing pungent tubercles; no cranial crests; 5) vomerine odontophores not visible except in large females, low, oblique; 6) males with vocal slits and subgular vocal sac; 7) first finger shorter than second; pads large, that on thumb smallest; discs broader than long; 8) fingers bearing narrow lateral fringes; 9) no ulnar tubercles except small antebrachial; 10) no tubercles on heel or outer tarsus; 1–2 tubercles on inner edge of tarsus; 11) two metatarsal tubercles, inner oval, 5–6 times size of outer; numerous supernumerary plantar tubercles; 12) toes bearing narrow lateral fringe, no webbing; toe pads as large as those of fingers; 13) above brown with darker brown markings—interorbital bar, scapular W, chevrons, facial and limb bars; venter brown; posterior thigh rich brown; 14) adults small, ten males 15.6–18.8 (\bar{x} = 17.5) mm, seven females 23.7–25.9 (\bar{x} = 24.5) mm SVL.

Eleutherodactylus incomptus is apparently related to the lowland *E. carvalhoi* Lutz, *E. croceinguinis* Lynch, and *E. martiae* Lynch but differs from each in being larger and not having the tympanum concealed. We are not aware of a comparable species on the trans-Andean slopes.

Description.—Head as wide as body in males, as wide as to narrower than in females; head wider than long; head width 35.2–38.4 (\bar{x} = 37.0, N = 10) percent SVL in males, 38.0–40.1 (\bar{x} = 38.7, N = 7) in females; snout short, E–N 66.7–80.0 (\bar{x} = 74.0, N = 10) percent eye length in males, 75.0–90.0 (\bar{x} = 82.8, N = 7) in females; nostrils weakly protuberant in males, not protuberant in females directed laterally; loreal region

weakly concave, sloping abruptly to lips; lips not flared; interorbital space flat, slightly broader than IOD; upper eyelid width 88.1–116.7 (\bar{x} = 97.1, N = 17) percent IOD; supratympanic fold thick, obscuring upper edge of tympanum; tympanum distinct, round to slightly higher than long, its length 25.0–31.8 (\bar{x} = 27.9, N = 10) percent eye length in males, 26.4–40.9 (\bar{x} = 33.4, N = 7) in females, separated from eye by distance equal tympanic diameter; temporal region nearly vertical; no enlarged tubercles on head except for some small postrostral tubercles; choanae moderate-sized, round, well anterior on palate, not concealed by palatal shelf of maxillary arch; vomerine odontophores not visible in males and small females, in adult females posteromedial to choanae, low, oblique, each a little smaller than a choana, bearing 2 teeth, separated medially by one odontophore width, tongue slightly longer than wide, posterior edge notched, posterior one-half of tongue not adherent to floor of mouth.

Skin of dorsum bearing low, flat warts, those toward posterior half of body more prominent than those on anterior half of body; no dorsolateral folds but indefinite, thin, fold may be present along upper flank; discoidal folds prominent; anal opening not enclosed in sheath; forearm lacking ulnar tubercles except for antebrachial tubercle; palmar tubercle bifid, smaller than oval thenar tubercle; numerous supernumerary palmar tubercles, none as large as subarticular tubercles; subarticular tubercles round, elevated, non-conical; fingers bearing narrow lateral fringes; all fingers bearing broad discs on broadly dilated pads, that of thumb more or less round, others broader than long; pads rounded apically.

No conical tubercles on heel, knee, or outer edge of tarsus; inner edge of tarsus bearing 1–2 elongate tubercles just proximal to inner metatarsal tubercle; inner metatarsal tubercle oval, non-compressed, its length 1.5 times its width, 5–6 times size of subconical outer

metatarsal tubercle; numerous plantar supernumerary tubercles, arranged in rows along metatarsals; subarticular tubercles round, elevated, non-conical to subconical; toes bearing narrow lateral fringes but no basal webbing; all toes bearing broad discs on pads, pads broader than long, those on toes III–V larger than those of I and II, pads rounded apically; heels of flexed hind legs touch; heel of adpressed hind leg reaches anterior edge of eye; shank 47.3–52.0 (\bar{x} = 49.7, N = 10) percent SVL in males, 46.7–49.6 (\bar{x} = 48.1, N = 7) in females.

Color in life.—Dorsum tan (olive-tan, reddish tan or brown in some) with darker brown markings; venter gray in most, dull brown or dirty cream with brown flecks in some individuals; iris dull bronze to gray with median horizontal reddish brown streak. One individual had a white snout.

Measurements of holotype in mm.—SVL 18.8; shank 9.1; head width 7.2; head length 7.1; upper eyelid width 2.4; IOD 2.1; tympanum length 0.8; eye length 3.0; E–N 2.0.

Etymology.—Latin, meaning unadorned; in reference to the drab pattern and lack of distinctive features.

Distribution and ecology.—This small inconspicuous frog occurs at elevations of 1410–1910 m on the eastern face of the Andes in Provincia Napo, Ecuador; it also is known from 1270 m in the Pastaza Valley, Provincia Pastaza, Ecuador. All specimens have been found in cloud forest areas, where they are most frequently encountered at night on leaves of herbs or low bushes in clearings or at the forest edge. One was on the forest floor by day.

Eleutherodactylus inusitatus new species

Fig. 3G

Holotype.—KU 166066, an adult female, taken at the Río Jatuntinahua, 10 km SE Cuyujúa, Provincia Napo, Ecuador, 2160 m, on 21 March 1975 by the incomparable John E. Simmons.

Paratypes.—CAS-SU 8279, SE of Ca-

yambe, Agua Caliente, on Río San Pedro, Provincia Napo, Ecuador; KU 120099, Abitagua, \approx 8 km (airline) NW Mera, Provincia Pastaza, Ecuador, 1300 m.

Diagnosis.—1) skin of dorsum sagegreened, that of venter coarsely areolate; 2) tympanum prominent, its length $\frac{1}{2}$ that of eye; 3) snout subacuminate in dorsal view, protruding in lateral profile, tip pointed; canthus rostralis sharp; 4) upper eyelid slightly narrower than IOD, bearing a conical tubercle; no cranial crests; 5) vomerine odontophores oval in outline; 6) males not known; 7) first finger shorter than second; fingers II–IV bearing large pads; discs broader than long; 8) fingers bearing lateral fringes; 9) conical ulnar warts present; 10) knee, heel, and outer edge of tarsus bearing conical tubercles; 11) two metatarsal tubercles, inner oval, 6–7 times size of conical outer; numerous supernumerary plantar tubercles; 12) toes bearing lateral fringes, not webbed; toe pads as large as those of outer fingers; 13) creamy white with faint brown canthal mark; green above, white below in life; 14) adults small, two adult females 24.0–24.4 mm SVL.

Superficially, *E. inusitatus* resembles *E. galdi* (Jiménez de la Espada), but the latter has large warts interspersed on the areolations of the venter, cranial crests; it is nearly twice as large as *E. inusitatus* and has a truncate snout (in lateral profile). Ignoring the prominent conical tubercles on the eyelid, forearm, heel, and tarsus, *E. inusitatus* resembles the slightly larger *E. acuminatus* Shreve of the upper Amazon Basin in Colombia, Ecuador, and Perú.

Description.—(proportions of two adults only): Head broader than body, broader than long; head width 39.6–41.4 percent SVL; E–N 93.5–96.8 percent eye length; nostrils not protuberant, directed laterally; loreal region concave, sloping abruptly to lips; lips not flared; upper eyelid width 85.2–96.2 percent IOD, bearing numerous subconical tubercles and one large, conical tubercle; no cra-

niai crests, interorbital space flat; temporal region sloping; supratympanic fold thick, tuberculate; tympanum prominent, higher than long, separated from eye by 1.5 times its length; tympanum length 29.0–32.3 percent eye length; skin above, below, and behind tympanum bearing conical warts; choanae moderate-sized, round, not concealed by palatal shelf of maxillary arch; vomerine odontophores prominent, median and posterior to choanae, oval in outline, separated by distance slightly less than an odontophore width, each larger than a choana, bearing 2–4 teeth in a clump; tongue longer than wide, posterior edge feebly notched, posterior one-fourth not adherent to floor of mouth.

Skin of dorsum shagreened (smooth in CAS-SU 8279), bearing large warts laterally; flanks and limbs coarsely warty; no dorsolateral folds; discoidal folds prominent, well anterior to groin; pair of conical subanal warts ventrolateral to anus; no anal sheath; three elongate, conical warts proximal to subconical antebrachial tubercle, largest on elbow; outer edge of palm bearing subconical warts; thenar tubercle oval, smaller than large round (partially divided) palmar tubercle (palmar 4–5 times size of thenar); numerous small supernumerary palmar tubercles; subarticular tubercles larger than palmar supernumeraries, broader than long; fingers bearing prominent lateral fringes; all fingers bearing discs (broader than long) on dilated pads; pads on II–IV very large, that on thumb small; pads apically rounded.

One or two conical tubercles on knee, one elongate tubercle (calcar) on heel; 2–3 smaller, conical tubercles on outer edge of tarsus; inner metatarsal tubercle oval (length 1.5 times width), much larger than conical outer metatarsal tubercle; many supernumerary plantar tubercles; subarticular tubercles round, smaller than those of fingers; toes bearing lateral fringes, broad discs on large pads (pads of toes as large as those of fingers); heels of flexed hind legs over-

lap; shank 50.8–53.7 percent SVL.

In preservative, cream-white with thin brown canthal stripe, vague anal triangle; underside of tarsus and foot, ventral side of wrist peppered with brown.

Color in life.—Dorsum green with faint brown bars on limbs; venter white. One specimen (KU 120099, a juvenile female) had a narrow yellow labial stripe and pale lemon yellow groin, lower flanks, and hidden surfaces of hind limbs. In that specimen the iris was pale yellowish gray, whereas in the holotype, it was reddish brown.

Measurements of holotype in mm.—SVL 24.0; shank 12.2; head width 9.5; head length 9.0; upper eyelid width 2.5; IOD 2.6; tympanum length 1.0; eye length 3.1; E–N 3.0 The holotype is gravid.

Etymology.—Latin, *in-* (negative of) + *usitatus* (usual or common), meaning rare or uncommon.

Distribution and ecology.—This distinctive species is known from only three specimens from three localities: Abitagua, Provincia Pastaza, Río Jatuntinahua, Provincia Napo, and Agua Caliente, on the Río San Pedro, southeast of Cayambe, Provincia Napo, Ecuador. The first is in the Río Pastaza valley at 1300 m at the point where the river emerges from the Andean front. The Río Jatuntinahua is a tributary at 2160 m to the upper Río Papallacta. The Agua Caliente, on the Río San Pedro, is presumably in the vicinity of the Río Oyacachi. One specimen was on a leaf of a low herb along a small stream and another was on the leaf of an elephant ear (*Xanthosoma*); both frogs were in cloud forest at night.

CAS-SU 8279 and KU 166066 are gravid females. KU 120099 is a juvenile or young female (slight convolutions of oviduct, small eggs) 16.0 mm SVL.

Eleutherodactylus lacrimosus
(Jiménez de la Espada)

Cyclocephalus lacrimosus Jiménez de la Espada,

1875, Vert. Viaje al Pacífico . . . Batracios, pl. 3, figs. 5, 5 a-b [Holotype apparently lost, type-locality unknown].

Hylodes lacrimosus: Nieden, 1923, Das Tierreich 46:467.

Syrrophus calceus: Lutz and Kloss, 1952, Mem. Instit. Oswaldo Cruz, 50:647 (misapplication).

Eleutherodactylus lacrimosus: Gorham, 1966, Das Tierreich, 85:80; Lynch and Schwartz, 1972, Journ. Herpetol. 5:109-12.

Eleutherodactylus chalceus: Lynch, 1968, Herpetologica 24:292 (misapplication).

Diagnosis.—1) skin of dorsal surfaces very finely shagreened (or smooth), that of venter areolate; no dorsolateral folds; 2) tympanum prominent, directed dorso-laterally, round, its length 31-45 percent eye length; 3) snout rounded in dorsal view and lateral profile but bearing papilla at tip; canthus rostralis rounded; 4) upper eyelid narrower than IOD, lacking tubercles; no cranial crests; 5) vomerine odontophores prominent, oval, obliquely oriented; 6) males with vocal slits and subgular vocal sac; no nuptial pads; 7) first finger shorter than second; fingers long; pads narrow (largest on outer fingers), rounded apically; discs broader than long; 8) no lateral fringe or keel on fingers; 9) no ulnar tubercles except for small antebrachial; 10) no tubercles on tarsus or heel; 11) two metatarsal tubercles, inner elongate, 5-6 times size of conical outer; few supernumerary plantar tubercles; 12) toes bearing lateral keels, not webbed; pads small, outer pads as large as those on outer fingers; 13) cream (rarely) to golden brown (usually) above, with or without small dark brown spots, sometimes having pale interorbital bar; venter creamy white with fine brown punctations; limb bars sometimes vaguely indicated; 14) adults small: in lowland populations (below 800 m) males 16.1-20.0 (\bar{x} = 18.5 \pm 0.5, N = 18) mm, females 20.6-24.4 (\bar{x} = 22.5 \pm 0.5, N = 18) mm SVL; in Amazonian slope frogs (900-1100 m) males 19.6-23.7 (\bar{x} = 21.0 \pm 0.8, N = 11) mm, females 24.4-32.5 (\bar{x} = 27.0 \pm 3.0, N = 5) mm SVL.

Eleutherodactylus lacrimosus is most

similar to *E. bromeliaceus* Lynch and *E. petersi* Lynch and Duellman but is readily distinguished by lacking pungent tubercles on the upper eyelid and heel; the most distinctive features of *E. lacrimosus* include its round flat head and coloration (golden-brown frog).

Description.—See Lynch and Schwartz (1972).

Color in life.—Pale golden-brown above becoming pale yellow on flanks, upper lip, digits, and venter; vocal sac yellow; spotting (if present) medium brown; iris red to bright reddish brown; venter of juveniles and females creamy white.

Distribution and ecology.—*E. lacrimosus* ranges from northeastern Brasil west to Ecuador and south into northern Perú. In east-central Ecuador it extends to at least 1100 m (Mera, Provincia Pastaza); all other locality records are lowland sites. Specimens are frequently encountered in arboreal bromeliads by day; at night frogs are found on vegetation 1-2 m above the ground.

Remarks.—Lutz and Kloss' (1952) record of *Syrrophus chalceus* from Iuaretê, Estado Amazonas, Brasil, appears to be this frog. Specimens of *E. lacrimosus* from northwestern Provincia Pastaza, Ecuador, are significantly larger than those found in the Amazonian lowlands. The large examples of *E. lacrimosus* come from the only area of sympatry between *E. lacrimosus* and its smaller upland relative, *E. petersi*.

Eleutherodactylus lanthanites Lynch

Fig. 3H

Eleutherodactylus lanthanites Lynch, 1975, Contrib. Sci., Nat. Hist. Mus. Los Angeles Co., (272):10 [Holotype.—KU 146144, Santa Cecilia, Provincia Napo, Ecuador, 340 m].

Diagnosis.—1) skin of dorsum finely tuberculate with scattered larger warts, no dorsolateral folds, that of venter smooth; 2) tympanum prominent, its length $\frac{2}{3}$ eye length; 3) snout acuminate in dorsal view, rounded in lateral

profile; canthus rostralis sharp; 4) upper eyelid narrower than IOD, lacking elongate tubercles, no cranial crests; 5) vomerine odontophores prominent, oblique to subtriangular in outline; 6) males with vocal sac and slits, non-spinous nuptial pad on thumb; 7) first finger longer than second; digital pads large, non-emarginate; 8) fingers lack lateral fringes; 9) no ulnar tubercles; 10) conical tubercle on heel; row of indistinct tubercles along outer edge of tarsus; 11) two metatarsal tubercles, inner elongate, 5–6 times size of conical outer; few supernumerary plantar tubercles; 12) toes lack lateral fringes; toe pads as large as those of outer fingers; 13) brown above with darker brown markings; shank bars perpendicular to limb axis; posterior surfaces of thighs uniform brown; throat heavily spotted and marbled with brown, defining median white stripe; 14) adults moderate-sized, in lowland populations (below 800 m) males 21.7–26.0 mm, females 27.5–44.8 mm SVL; in Amazonian slope frogs (900–1490 m) males 23.9–27.9 ($\bar{x} = 26.3 \pm 1.6$, $N = 5$) mm, females 38.7–45.4 ($\bar{x} = 41.2$, $N = 4$) mm SVL.

Eleutherodactylus fitzingeri (Schmidt) and *E. gutturalis* Hoogmoed, Lynch and Lescure have similar gular patterns but lack the calcar on the heel and have longer legs; *E. fitzingeri* also has pronounced webbing of the toes.

Description.—See Lynch (1975b).

Color in life.—(Andean slope specimens): Dorsum tan (pinkish-, olive-) to brown with or without dark brown, reddish brown, olive-green, or dull red markings; in some individuals, lips barred creamy tan and black; canthal and supratympanic stripes black; posterior groin and anterior and posterior surfaces of thighs salmon to grayish brown; venter creamy white to creamy yellow with pinkish rose tint posteriorly in some individuals, mottled with gray in some individuals; bright yellow spots on posterior flanks in some individuals; iris bronze with median horizontal streak to copper.

Distribution and ecology.—*Eleutherodactylus lanthanites* is an abundant frog in the lowland rainforest in Ecuador and adjacent Colombia. It ascends the Andes in lower humid montane forest to 1440 m in southern Colombia and to 1490 m in Ecuador. In the lowlands the frogs occur on the forest floor by day and on low vegetation at night. In the Andes all specimens were on bushes or low trees (to 2 m) at night.

The small sample of *E. lanthanites* from the cloud forest suggests that slope frogs are significantly larger than lowland frogs.

Eleutherodactylus leoni Lynch

Fig. 4A

Eleutherodactylus leoni Lynch, 1976, *Herpetologica* 32:313 [*Holotype*.—KU 130870, taken on the N slope of the Nudo de Mojanda, Provincia Imbabura, Ecuador, 3400 m].

Diagnosis.—1) skin of dorsum shagreened, with many short ridges, scattered larger tubercles, no dorsolateral folds, that of venter areolate; 2) tympanum partially concealed beneath skin, its length $\frac{1}{2}$ – $\frac{2}{3}$ eye length; 3) snout subacuminate in dorsal view, angularly rounded (nearly truncate) in lateral profile; canthus rostralis moderately sharp; 4) upper eyelid narrower than IOD, bearing 2–4 conical tubercles; no cranial crests; 5) vomerine odontophores low, oblique; 6) males with vocal slits, subgular vocal sac; no nuptial pads; 7) first finger shorter than second; pads and discs on fingers II–IV, pads round; 8) fingers lack lateral fringes; 9) small ulnar tubercles present; 10) no enlarged heel tubercles; outer tarsal tubercles conical; ridge on inner edge of tarsus; 11) two metatarsal tubercles, inner elongate, twice size of round outer; supernumerary plantar tubercles small; 12) toes bearing narrow lateral keels, no web; 13) brown above with darker markings; limb bars narrow, oblique; venter gray to brown with cream spots; white and/or colorless areas in axilla, groin, and con-

cealed surfaces of thigh and shank salmon or bright red in life; 14) adults small, males 13.0–18.3 mm, females 19.7–25.0 mm SVL.

Eleutherodactylus leoni is most similar to *E. pyrromerus* Lynch but differs in having large choanae, smaller vomerine odontophores, more than one conical tubercle on the upper eyelid, less conical postriatal tubercles, and broader digital pads.

Description.—See Lynch (1976a).

Color in life.—Dorsum brown to reddish brown with dark gray, black, tan, and cream markings; lips barred cream and brown; venter gray with white flecks and/or small yellow spots; throat with yellowish wash; groin and lower flanks fleshy gray to salmon with orange yellow spots; hidden surfaces of thighs and groin gray to salmon in smaller individuals, red in large females; iris powder blue (with or without green tint), with black flecks and brown horizontal streak.

Distribution and ecology.—This frog is a small terrestrial inhabitant of upper humid montane forest at elevations of 2710–3400 m on the Pacific slopes of the Andes in Ecuador and 2540–2700 m on the Amazonian slopes in Colombia and Ecuador. On the Amazon slopes of Ecuador, *E. leoni* is known only from the upper Río Chingual drainage. All specimens from the Amazon slopes in Ecuador were found beneath logs and rocks in clearings in cloud forest.

Eleutherodactylus leucopus Lynch

Eleutherodactylus leucopus Lynch, 1976, Proc. Biol. Soc. Washington 88:351 [*Holotype.*—USNM 197927, Santa Barbara, Provincia Napo, Ecuador, 2590 m].

Diagnosis.—1) skin of dorsum feebly granulate, no dorsolateral folds, that of venter coarsely areolate; 2) tympanum prominent, its length $\frac{1}{2}$ – $\frac{1}{3}$ eye length; 3) snout subacuminate in dorsal view (tip pointed), protruding in lateral profile; canthus rostralis sharp; 4) upper eyelid slightly narrower than IOD, lacking tubercles; low cranial crests present;

5) vomerine odontophores prominent, oval to triangular in outline; 6) males with vocal slits, subgular vocal sac; no nuptial pads; 7) first finger shorter than second; all fingers with broad pads; 8) fingers lack lateral fringes; 9) small ulnar tubercles; 10) heel and tarsus bearing small non-conical tubercles; inner tarsal fold ridge-like; 11) two metatarsal tubercles, inner oval, outer non-conical, $\frac{3}{4}$ – $\frac{1}{2}$ size of inner; plantar surface areolate; 12) toes bearing prominent lateral fringes, no web; 13) dark gray above, venter cream flecked with gray; fingers and toes pale cream; posterior thighs, groin dark gray; 14) adults moderate-sized, males 30.0–37.8 mm, females 42.3–44.0 mm SVL.

Eleutherodactylus leucopus is most similar to *E. acerus* Lynch and Duellman (described above); *E. leucopus* differs from *E. acerus* in having granular skin (not smooth), inner tarsal tubercles (none), and cream inner digits (brown).

Description.—See Lynch (1976c).

Distribution and ecology.—*E. leucopus* is known from the valley of the Río Chingual, at elevations between 2440 and 2700 m in Ecuador and Colombia. The late James A. Peters and his associates found the frogs beneath logs in clearings “in good forest.” At night, specimens were found on leaves and branches in heavy undergrowth (? secondary forest) in upper montane cloud forest. In July 1977, Lynch collected at El Carmelo and Santa Bárbara, as well as above El Carmelo. The forests mentioned in Peter’s field notes were largely cleared; no specimens of *E. leucopus* were found, although several other species of *Eleutherodactylus* were encountered.

Eleutherodactylus lividus new species

Fig. 4B

Holotype.—KU 166005, an adult female, taken 11 km ESE Papallacta, Provincia Napo, Ecuador, 2660 m, on 22 March 1975 by William E. Duellman and Linda Trueb.

Paratypes.—KU 155450, 166006–07, topotypes; KU 165992, 165004, 12 km ESE Papallacta, 2630 m.

Diagnosis.—1) skin of dorsum finely areolate, that of venter coarsely areolate; 2) tympanum prominent, its length $\frac{3}{8}$ – $\frac{1}{2}$ eye length; 3) snout rounded to subacuminate in dorsal view, rounded in lateral profile, bearing papilla at tip; canthus rostralis sharp; 4) upper eyelid narrower than IOD, bearing one conical tubercle; low cranial crests present; 5) vomerine odontophores prominent, rounded to slightly oblique; 6) males lacking vocal sac and slits; 7) first finger shorter than second; fingers II–IV bearing dilated pads; discs broader than long; 8) fingers bearing lateral keels; 9) ulnar fold bearing subconical tubercles; 10) heel and tarsus bearing pungent, subconical tubercles; 11) two metatarsal tubercles, inner oval, 6–8 times size of outer; numerous supernumerary plantar tubercles; 12) toes bearing lateral fringes, not webbed; toe pads as large as those of outer fingers; 13) gray above with brown suffusion on face, sacrum and lower limbs, dorsum flecked with black; venter dull cream flecked with brown; posterior thigh black with dull yellow reticulation; 14) adults moderate-sized, two males 18.2–20.4 mm, three females 32.9–35.0 mm SVL.

Eleutherodactylus lividus is similar to *E. acerus* Lynch and Duellman (described above) but differs in having conical tubercles on the eyelid, heel, and tarsus, and more coarse warts on the flanks. In addition, *E. lividus* is smaller than *E. acerus* (three males 25.0–34.0 mm, one adult female 45.1 mm SVL) and males lack vocal sac and slits.

Description.—Head narrower than body, wider than long; head width 37.2–37.4 percent SVL in two males, 37.7–40.3 (\bar{x} = 38.6, N = 4) in females; nostrils not protuberant, directed dorsolaterally; E–N 80.8–97.4 (\bar{x} = 87.1, N = 6) percent eye length; loreal region of canthus rostralis concave, sloping abruptly to lips; lips not flared; low cranial crests (palpable); upper eyelid bearing one

conical tubercle, its width 70.8–96.8 (\bar{x} = 84.4, N = 6) percent IOD; tympanum directed dorsolaterally, prominent, its upper edge concealed by thick supratympanic fold, separated from eye by tympanum length; tympanum round, its length 29.8–41.9 (\bar{x} = 34.9, N = 6) percent eye length; several small, round, subconical postrictal tubercles; choanae small, round, not concealed by palatal shelf of maxillary arch; vomerine odontophores median and posterior to choanae, each the size of a choanae, round or somewhat oblique, elevated, bearing a clump of 2–4 teeth, separated medially by distance equal an odontophore width; tongue broader than long, its posterior edge notched, posterior two-fifths not adherent to floor of mouth.

Skin of dorsum finely areolate (without ridges) becoming more coarsely areolate on flanks and venter; discoidal folds not prominent; no anal sheath or enlarged tubercles; limbs areolate except posterior surface of thigh and underside of shank; ulnar fold present, bearing subconical tubercles, antebrachial largest; palmar tubercle bifid, larger than oval thenar tubercle; numerous supernumerary palmar tubercles, all low; subarticular tubercles round (except for basal on IV—longer than wide), nonconical, elevated; fingers bearing ill-defined lateral fringes; all fingers with discs (broader than long) on dilated, apically round pads; pad on thumb scarcely wider than digit, those on II–IV twice as wide as digit.

Heel bearing 2–3 subconical tubercles, 2–3 subconical tubercles on outer edge of tarsus; inner tarsal fold a thickened ridge with a low tubercle; inner metatarsal tubercle oval (length twice width), not compressed, 6–8 times size of round, subconical outer; numerous supernumerary plantar tubercles, none prominent except for conical tubercles at bases of toes II–IV; subarticular tubercles round, pungent, larger than any supernumerary tubercle; toe fringes present, more definite than those of hand, no webbing; toes with discs (broader

than long) on dilated pads (at least twice width of digit below pad), rounded apically; heels of flexed hind limbs overlap; heel of adpressed hind leg reaches eye; shank 47.2–52.8 (\bar{x} = 49.4, N = 6) percent SVL.

In preservative, gray above with brown interorbital bar, some brown suffusion on face, sacrum, and lower limbs; dorsum flecked with black; venter dull cream with brown-black flecks laterally; underside of shank cream with black spots; posterior thigh surfaces black with dull yellow reticulation ventrally; flank and anterior surfaces of thighs dark gray with dull yellow reticulation breaking up into small dark spots; labial bar, canthal-supratympanic stripe ill-defined.

Color in life.—Dorsum brown (pale green in one individual); venter cream with brown or black flecks or pale gray; blue or grayish blue in groin and, in some individuals, on posterior surfaces of thighs; iris bronze.

Measurements of holotype in mm.—SVL 35.0; shank 16.6; head width 13.2; head length 11.8; upper eyelid width 3.8; IOD 4.2; tympanum length 1.8; eye length 4.3; E–N 3.8. The holotype is gravid.

Etymology.—Latin, meaning blue or bluish, in reference to the concealed colors in the groin.

Distribution and ecology.—This species is known only from the Papallacta Valley on the eastern face of the Andes in Provincia Napo, Ecuador, where it occurs at elevations of 2135–2750 m. All individuals were found in cloud forests; one was under a rock by day, and the others were on the leaves of herbs and low bushes at night.

Remarks.—Although most similar to, and readily confused with *E. acerus* (unless compared), *E. lividus* seems to be equally related to *E. glandulosus* and *E. leucopus*. *Eleutherodactylus lividus* is sympatric with *E. acerus* and *E. glandulosus*; all three are allopatric to *E. leucopus*. The four form a cluster of species distributed in cloud forest on the eastern face of the Andes in northern

Ecuador and have no other apparent close relatives, although *E. percultus* Lynch from the Abra de Zamora in southern Ecuador may be related.

Eleutherodactylus nigrogriseus
(Andersson)

Fig. 4C

Pseudohyla nigrogrisea Andersson, 1945, Arkiv für Zoologi 37A(2):87 [*Syntypes.*—NHRM 1905 (1 adult and 5 juveniles) collected at Baños, Provincia Tungurahua, Ecuador].
Eleutherodactylus nigrogriseus: Lynch, 1969, Bull. So. California Acad. Sci. 68:219–24.

Diagnosis.—1) skin of dorsum shagreened (with scattered tubercles, no dorsolateral folds), that of venter coarsely areolate; 2) tympanum prominent, its length $\frac{1}{4}$ – $\frac{1}{3}$ eye length; 3) snout subacuminate in dorsal view, rounded to truncate in lateral profile; canthus rostralis sharp; 4) upper eyelid lacking tubercles, its width about equal IOD; no cranial crests; 5) vomerine dentigerous processes small, triangular in outline; 6) males lack vocal sac and slits; no nuptial pad; 7) first finger shorter than second; fingers II–IV bear broad, apically rounded pads; 8) fingers with ill-defined lateral fringes; 9) no ulnar tubercles (except antebrachial); 10) heel with one conical tubercle, none on tarsus; 11) two metatarsal tubercles, inner oval, 4 times size of round outer; many small supernumerary plantar tubercles; 12) toes bearing lateral fringes, no web; toe pads as large as those of fingers; 13) dorsum brown with darker mottling; venter tan to gray mottled with brown; posterior flank, groin, anterior and posterior surfaces of thighs, and concealed shank dark brown to black with large white (yellow in life) spots; iris red in life; 14) adults moderate-sized, males 19.3–26.0 (\bar{x} = 22.7, N = 20) mm, two females 28.5–29.4 mm SVL.

In life, *E. nigrogriseus* cannot be confused with other species but in preservative, the bold yellow spots on the flank, groin, and thighs are white; *E. nigrogriseus* might be confused with *E. eri-*

phus Lynch and Duellman or *E. spinosus* Lynch. Both have more warty skin and prominent tubercles along the outer edge of the tarsus.

Description.—See Lynch (1969b).

Color in life.—Dorsum tan, olive-green, or nearly black, with black markings on limbs and back; groin and anterior and posterior surfaces of thighs black with bright yellow spots (discrete in adults, diffuse in juveniles); venter tan to gray with cream or white flecks, brown flecks in some; iris red.

Distribution and ecology.—Most specimens of *E. nigrogriseus* are from the Río Pastaza Valley (1180–1800 m) and slopes of the Andes in southern Ecuador (Provincia Morona-Santiago, 2195–2835 m), but one individual is from the Cordillera del Dué (1150 m) in northern Ecuador. In these cloud forests the frogs are found on low vegetation and rocks, usually along streams, at night.

Eleutherodactylus nigrovittatus

Andersson

Fig. 4D

Eleutherodactylus nigrovittatus Andersson, 1945, Arkiv für Zoologi 37A(2):33 [*Holotype.*—NHRM (not examined), Abitagua, Río Pastaza, Provincia Tungurahua, Ecuador].

Diagnosis.—1) skin of upper surfaces finely shagreened with small tubercles and folds (including incomplete dorso-lateral folds), that of venter smooth; 2) tympanum distinct, its length $\frac{1}{2}$ eye length; 3) snout acuminate in dorsal view, pointed (males) or rounded (females) in lateral profile, fleshy swelling of lip in adult male; canthus rostralis obtuse, concave; 4) upper eyelid narrower than IOD, lacking enlarged tubercles; no cranial crests; 5) vomerine odontophores prominent, oval, extending laterally to level of choanae; 6) males lacking vocal sac, slits, and nuptial pads; 7) first finger longer than second; fingers bearing elongate discs (as long as wide), digits not expanded into pads; 8) fingers

lack lateral fringes; 9) no ulnar tubercles; 10) minute tubercles on heel and outer edge of tarsus; 11) two metatarsal tubercles, inner oval, twice size of round outer; no supernumerary plantar tubercles; 12) toes lack lateral fringes, no webbing; toes bearing expanded, apically pointed pads; discs as long as wide; 13) brown above with darker brown suprainguinal spots, anal triangle, underside tarsi and feet; faint canthal-supratympanic stripe, labial, and limb bars; venter cream; posterior surfaces of thigh brown with small cream spots; 14) adults small to moderate-sized: lowland (< 600 m) males 13.3–19.4 (\bar{x} = 17.0, N = 9) mm, females 19.7–22.1 (\bar{x} = 20.9, N = 9) mm SVL; slope population (900–1935 m) males 17.2–24.6 (\bar{x} = 21.4, N = 33) mm, females 25.0–30.5 (\bar{x} = 27.4, N = 21) mm SVL.

Eleutherodactylus nigrovittatus is most likely confused with specimens of the leptodactylines *Adenomera*, small *Leptodactylus*, and *Vanzolinius*. None of these has pointed discs and pads on the toes as well as lacking lateral fringes on the digits, nor does any other species of *Eleutherodactylus* in northern South America.

Description.—See Andersson (1945).

Color in life.—Dorsum gray, tan, reddish brown, or orange; inguinal spots and anal triangle black; labial and limb bars dark brown; venter gray or lemon yellow with black and white mottling on throat; orange suffusion in groin, iris dull bronze heavily suffused with black.

Distribution and ecology.—*Eleutherodactylus nigrovittatus* occurs in the upper Amazon Basin in Ecuador and Perú; in Ecuador it ascends the Andes in cloud forest to 1935 m. The frogs are active on the forest floor by day; a few have been found on low herbs at night.

Eleutherodactylus ockendeni

(Boulenger)

Hylodes ockendeni Boulenger, 1912, Ann. Mag. Nat. Hist. (8)10:187 [*Syntypes.*—BM 1907.5.7.19–21/RR 1947.2.16.88–90, La

Union, Río Huacamayo, Carabaya, Departamento Puno, Perú, 600 m].

Hylodes hylaeformis Melin, 1941, Medd. Göteborgs Mus. Zool. Avdel. 88:48 [*Holotype* (not examined), Roque, Departamento San Martín, Perú]. Synonymy *vide* Lynch (1980).

Syrhophus calcaratus Andersson, 1945, Ark. Zool. 37A:27 [*Holotype*.—NHRM 1941, Río Cosanga near Archidona, Provincia Napo, Ecuador, 800 m]. Synonymy *vide* Lynch (1974).

Eleutherodactylus melini Bokermann, 1958, Herpetologica 14:95 [replacement name for *Hylodes hylaeformis* Melin, 1941, non *Phyllobates hylaeformis* Cope, 1975].

Eleutherodactylus anderssoni Lynch, 1968, Herpetologica 24:292 [replacement name for *Syrhophus calcaratus* Andersson, 1945, non *Hylodes calcaratus* Boulenger, 1908].

Eleutherodactylus ockendeni is a frog of lowland rainforests in the upper Amazon Basin from southern Colombia to southern Perú (Lynch, 1974, 1980). Like *E. croceinguinis*, *E. ockendeni* invades very low cloud forests in the lower Pastaza Trench. Unlike *E. croceinguinis*, *E. ockendeni* is uncommon in low cloud forests.

Eleutherodactylus pastazensis

Andersson

Eleutherodactylus pastazensis Andersson, 1945, Arkiv för Zoologi 37A(2):37 [*Syntypes*.—NHRM 1918, 2 individuals, the larger from Yanguilla, the smaller from Mount Tungura (= ? Tungurahua), 1840 m, Río Pastaza, Provincia Tungurahua, Ecuador, collected in December 1937 by Wm. Clarke-MacIntyre].

Diagnosis.—1) skin of upper surfaces smooth with non-pungent warts on posterior back, that of venter coarsely areolate; 2) tympanum distinct, its length $\frac{1}{4}$ – $\frac{1}{2}$ eye length; 3) snout subacuminate in dorsal view, protruding or angularly rounded in lateral profile, papilla at tip; canthus rostralis obtuse; 4) upper eyelid narrower than IOD, lacking pungent tubercles; no cranial crests; 5) vomerine odontophores low, not prominent, oblique; 6) males with vocal slits and subgular vocal sac, non-spinous nuptial pads on thumb; 7) first finger shorter than second; fingers bearing large pads

(largest on III–IV); discs broader than long; 8) fingers bearing indistinct lateral fringes; 9) ulnar tubercles absent; 10) heel and tarsus lacking pungent tubercles; 11) two metatarsal tubercles, inner oval, 4–5 times size of round outer; supernumerary plantar tubercles numerous, ill-defined; 12) toes bearing lateral fringes, no webbing; toe pads smaller than those of outer fingers; 13) brown above with indefinite darker brown flecking, sometimes forming pattern of chevrons, interorbital bar, and limb bars; venter cream or brown; concealed thigh uniform pale brown or bearing indefinite cream and brown marbling; 14) adults small to moderate in size, one male 19.5 mm, two females 30.9–31.7 mm SVL.

Eleutherodactylus pastazensis is a remarkably nondescript frog. We are aware of only four examples, all collected 40 years ago, lacking color descriptions in life or while freshly preserved. In many respects, *E. pastazensis* resembles *E. unistrigatus* but is readily distinguished in having a papilla at the tip of the snout, smaller tympana, non-spinous nuptial pad in males, and more distinct fringes on the digits. Although the color pattern of *E. unistrigatus* is variable, the lack of pattern (or reduced pattern) of *E. pastazensis* is beyond the range of variation in *E. unistrigatus*; the nearly uniform brown posterior thigh of *E. pastazensis* (except in CAS-SU 5084) is unlike the mottled concealed thigh of *E. unistrigatus* (occasionally unpigmented).

Description.—Head slightly narrower than body; head broader than long; head width 38.0–39.4 (\bar{x} = 38.7) percent SVL; canthus rostralis obtuse, relatively straight; nostrils weakly protuberant, directed dorsolaterally; loreal region weakly concave, sloping abruptly to lips; lips not flared; upper eyelid 73.0–87.5 (\bar{x} = 81.4) percent IOD, bearing small, non-pungent warts; interorbital space flat, no cranial crests; supratympanic fold present, not obscuring tympanic annulus; tympanum distinct, round in outline, its length 25.9 percent eye length in male,

31.6–46.2 in two females; tympana of male (CAS-SU 5065) less distinct than in three females; tympanum smaller than pad of third finger, separated from eye by tympanum diameter; choanae relatively small, round, not concealed by palatal shelf of maxillary arch when viewed from directly above; vomerine odontophores median and posterior to choanae, oblique, low, bearing clump or slanted row of 1–4 teeth; odontophores widely separated medially; tongue longer than wide, posterior $2/5$ not adherent to floor of mouth.

Skin of dorsum and head smooth, that on posterior back bearing scattered or dense low, non-pungent warts; no dorsolateral folds; discoidal folds prominent posteriorly, well anterior of groin; no ulnar tubercles (even antibrachial not apparent); palmar tubercle bifid, slightly larger than oval thenar tubercle; supernumerary palmar tubercles numerous, small, non-pungent; subarticular tubercles round, pungent, distal tubercles on fingers III–IV least pungent; fingers bearing lateral fringes (most distinct in CAS-SU 5084, somewhat desiccated); fingers bearing discs (broader than long) on dilated pads, pads of III and IV largest (at least twice digit width), that on thumb smallest (II intermediate in size); pads apically rounded.

Heel and tarsus lacking tubercles; inner metatarsal tubercle not compressed, length twice width; outer metatarsal tubercle round $1/4$ – $1/2$ size of inner; plantar surface bearing indistinct supernumerary tubercles arranged in rows; subarticular tubercles round, pungent (distal tubercles much less so), smaller than subarticular tubercles of fingers; toes bearing lateral fringes, not webbed; toe pads like those of fingers but smaller than those of fingers III–IV; hind limbs short, shank 46.9–50.8 (\bar{x} = 48.3) percent SVL.

In preservative, *E. pastazensis* is pale brown to reddish brown above with dark-brown or black flecking forming ill-

defined interorbital bar, chevrons, limb bars, and diffuse marbling on upper flanks. Canthal and supratympanic stripes are present but not distinct. The venter is cream, stippled (punctations) with brown. The posterior flanks and concealed surfaces of thighs and shanks are heavily peppered with brown. CAS-SU 5084 has some pale cream on the upper edge of the posterior thigh; the cream area is reticulated with reddish brown markings extending from the top of the thigh.

Measurements of larger syntype.—SVL 30.9; shank 14.5; head width 12.0; head length 9.8; upper eyelid 3.1; IOD 3.7; tympanum 1.2; eye length 3.8; E–N 3.3. The specimen is a gravid female.

Natural history.—Both adult females are gravid. CAS-SU 5084 was collected in September 1939; NHRM 1918 (larger) was collected in December 1937. The smaller syntype is a juvenile female 23.3 mm SVL. The male (CAS-SU 5065) has a distended vocal sac and nuptial pads; the testes are relatively small and cream colored.

Remarks.—The larger individual included under NHRM 1918 was described and illustrated by Andersson (1945). This individual is here designated as the lectoholotype.

The rarity of *E. pastazensis* is inexplicable. All four known individuals were collected by Wm. Clark-MacIntyre. The University of Michigan Museum of Zoology also purchased specimens from him, but no specimens were found in a survey of that collection. Most collectors operating in Ecuador in the past 20 years have neglected the Baños area in the Pastaza valley while opting for the richer habitats at lower elevations or along other routes into the Amazon Basin. Collecting by individuals searching for frogs may well reveal *E. pastazensis* to be restricted to the upper Pastaza valley.

Distribution.—Known only from the upper Río Pastaza valley in the vicinity of Baños at elevations of 1800–1840 m.

Eleutherodactylus peruvianus (Melin)

Fig. 4E

Hylodes peruvianus Melin, 1941, Medd. Göteborgs Mus. Zool. Avd. 88:43 [*Holotype*.—NHMG 490, adult female, taken at Roque, Departamento San Martín, Perú].

Eleutherodactylus peruvianus: Gorham, 1966, Das Tierreich 85:91.

Eleutherodactylus conspicillatus (part): Lynch, 1975, Contrib. Sci., Nat. Hist. Mus. Los Angeles Co. (272):3.

Lynch (1980) and Duellman and Toft (1979) advocated recognition of a lowland frog found in western Brasil, southern Ecuador, and Perú, that is similar to *E. conspicillatus*; they applied the name *E. peruvianus* (Melin) which Lynch (1975b) had placed in the synonymy of *E. conspicillatus*. Lynch (1980) noted that the two putative species are very similar but presumably sympatric over central Perú. We have assigned specimens found on the lower Andean slopes in southern Colombia and Ecuador, as well as from several questionable localities in lowland eastern (Napo and Pastaza provinces) Ecuador to *E. peruvianus* rather than describe the frogs as a new species. Resolving the specific status of these frogs will require considerable field work in areas of southern Ecuador and northern Perú; assigning them to *E. peruvianus* is not entirely satisfactory but seems preferable to proposing another name at present. The following account applies only to what we refer to as "slope populations."

Diagnosis.—(based on Andean slope specimens): 1) skin of dorsum shagreened with scattered warts and interrupted (albeit complete) dorsolateral folds, that of venter smooth; 2) tympanum prominent, its length $\frac{2}{3}$ – $\frac{1}{2}$ eye length; 3) snout rounded to subacuminate in dorsal view, rounded in lateral profile; canthus rostralis sharp; 4) upper eyelid broader than IOD, not bearing pungent warts; no cranial crests; 5) vomerine odontophores prominent, triangular in outline; 6) males with vocal slits and subgular vocal sac, white, non-

spinous nuptial pads on thumbs; 7) first finger much longer than second; fingers III–IV bearing small pads; discs broader than long; 8) fingers bearing lateral keels; 9) no ulnar tubercles; 10) no tubercles on knee, heel, or tarsus aside from slight tubercle on inner edge of tarsus; 11) two metatarsal tubercles, inner oval, 6 times size of outer; 2–3 supernumerary plantar tubercles; 12) toes bearing lateral keels, not webbed; toe pads slightly larger than those of fingers III–IV; 13) dorsum brown with darker chevrons, facial and limb bars; venter cream with brown flecks, throat heavily peppered with brown, bearing thin gular stripe; posterior thigh brown with small cream flecks to brown with large cream spots; undersides of limbs cream dusted with brown; 14) adults moderate-sized, males 29.2–35.8 (\bar{x} = 31.8 \pm 1.4, N = 10) mm, females 38.6–46.4 (\bar{x} = 42.3 \pm 1.4, N = 10) mm SVL.

These frogs differ from *E. conspicillatus* (found at lower elevations) in having moderate to heavy brown markings on the throat, the labial bars and canthal-supratympanic stripes are evident through the masking on the face, and in being slightly larger. They also differ in having scattered enlarged tubercles on the shagreened skin of the dorsum.

Description. — (slope populations): Head wider than body, wider than long; head width 37.0–44.0 (\bar{x} = 40.1, N = 20) percent SVL; E–N 86.1–108.3 (\bar{x} = 96.2, N = 19) percent eye length; nostrils weakly protuberant, directed laterally; loreal region weakly concave, sloping abruptly to lips; lips very weakly flared; upper eyelid bearing small tubercles, none pungent; upper eyelid width 79.2–122.0 (\bar{x} = 91.0, N = 19) percent IOD; cranial crests not present but edges of frontoparietals slightly elevated; tympanum round to slightly higher than long, directed laterally with slight dorsal vector, upper edge concealed by supratympanic fold; tympanum length 38.8–57.9 (\bar{x} = 47.2, N = 19) percent eye length, separated from eye by its length;

postrictal tubercles small, conical; choanae moderate-sized, not concealed by palatal shelf of maxillary arch; vomerine odontophores medial and posterior to choanae, elevated, triangular in outline, separated medially by distance equal one-half width of an odontophore, each 1.5 times size of a choana, bearing slanted row of 8–9 teeth; tongue longer than wide, posterior border notched, posterior $\frac{1}{2}$ – $\frac{1}{4}$ not adherent to floor of mouth.

Skin of dorsum shagreened and bearing slightly larger warts and interrupted dorsolateral fold (series of warts from eye to above groin); several small warts behind eye (above supratympanic fold) and on flanks; skin of limbs shagreened; no supra-anal warts or anal sheath; discoidal folds prominent; skin below and lateral to vent bearing flat warts; no ulnar tubercles; palmar tubercle bifid, larger than oval thenar tubercle, supernumerary palmar tubercles not pungent, scarcely evident; subarticular tubercles longer than wide, conical; fingers bearing lateral keel; small pads, largest on fingers III–IV, those of I–II scarcely expanded; discs broader than long; pads rounded apically.

No tubercles on heel or outer edge of tarsus; inner edge of tarsus bearing indistinct tubercle; inner metatarsal tubercle oval, length twice width, not compressed, 6 or more times size of subconical outer; 2–3 supernumerary plantar tubercles (base of toes II, III, sometimes IV), indistinct; subarticular tubercles longer than wide, non-conical; toes bearing lateral keels, no web; pads of toes slightly larger than those of outer fingers (pads of toes I–II about same size as pads of fingers III–IV); hind legs long, heels of flexed hind legs broadly overlap; heel of adpressed hind leg reaches beyond snout tip; shank 50.9–69.8 (\bar{x} = 63.1, N = 23) percent SVL.

In preservative, brown (pale to dark) above with darker brown chevrons and slanted flank bars, interorbital bar, canthal-supratympanic stripe, and labial bars; lower flanks pale brown; limb bars narrow (less than half width of inter-

spaces), oblique; anal triangle prominent; posterior surfaces of thighs brown with small cream flecks to relatively large cream spots; throat heavily dusted with brown and bearing narrow pale gular stripe; breast and belly more sparsely peppered with brown (appearing cream in most individuals; throat paler in many individuals as well); undersides of limbs dusted with brown, underside of shank bearing colorless spots.

Color in life.—(specimens from Río Azuela and Río Salado, Provincia Napo, Ecuador): Dorsum brown to reddish brown with dark brown chevrons on body and diagonal bars on limbs; anterior and posterior surfaces of thighs dark brown with small orange-red spots; belly white or creamy yellow with black or brown flecks; throat, groin, and ventral surfaces of thighs with reddish buff tint; iris reddish-copper.

John E. Simmons' specimens from the Cordillera del Condor were as follows: dorsum tan or brown with dark brown to black markings; post-tympanic spot black; limbs barred with white, venter mottled gray and tan or white. Simmons' brief and seemingly contrasting notes probably stem from confusing *E. condor* and *E. peruvianus* in the field with the attendant assumption that the smaller *E. peruvianus* were juveniles of the larger frog that he found (*E. condor*).

Distribution and ecology.—*Eleutherodactylus peruvianus* occurs in the upper Amazon Basin in western Brasil, southern Ecuador, and eastern Perú and in cloud forests on the eastern slopes of the Andes to 1910 m in Ecuador and Perú. It is primarily a terrestrial species, individuals being found in the forest floor by day and night; a few have been found on low vegetation at night.

Eleutherodactylus petersi new species

Fig. 4F

Holotype.—KU 143508, adult male, taken 16.5 km NNE Santa Rosa, Provincia Napo, Ecuador, 1700 m, 17 October

1971 by William E. Duellman.

Paratypes.—KU 143509–12, topotypes collected 18–19 October 1971 by W. E. Duellman and J. T. Collins.

Diagnosis.—1) skin of dorsum smooth, no dorsolateral folds, that of venter coarsely areolate, discoidal folds present; conical tubercle on eyelid; 2) tympanum prominent, round, its length $\frac{1}{2}$ that of eye; 3) snout round in dorsal view, truncate in lateral profile, bearing papilla at tip; snout short; 4) interorbital space flat, broader than upper eyelid; 5) vomerine odontophores low, oblique; 6) males with large, subgular vocal sac and vocal slits; 7) first finger shorter than second; all fingers long, bearing discs on broadly dilated, round apically, pads; 8) fingers bearing narrow lateral fringes; 9) no ulnar tubercles; 10) no tubercles on knee, heel, or outer edge of tarsus; inner tarsal fold bearing 2–3 tubercles; 11) two metatarsal tubercles, inner oval, 4 times size conical outer; plantar surface areolate; 12) toes bearing narrow lateral fringes, discs on broad pads; 13) pale cream with brown interorbital bar, canthal and supratympanic stripes; venter white; posterior thigh pale brown; pale green in life; 14) adults small, 35 males 14.5–19.9 mm, eight females 20.3–23.1 mm SVL.

Eleutherodactylus petersi is readily distinguished from all other species in the *unistrigatus* group on the basis of its very short snout, conical tubercles on the snout and upper eyelid (but none on the heel), and its long, slender digits bearing large pads. The frog is most similar to, and related to, *E. bromeliaceus* Lynch and *E. lacrimosus* (Jiménez de la Espada). *Eleutherodactylus bromeliaceus* has conical tubercles on the heel and outer edge of the tarsus; *E. lacrimosus* lacks tubercles on the upper eyelid.

Description.—Head as broad as body, wider than long; head width 35.6–42.5 (\bar{x} = 37.6, N = 25) percent SVL; snout very short, E–N 66.1–100.0 (\bar{x} = 80.2, N = 25) percent eye length; nostrils weak-

ly protuberant, directed dorsolaterally; loreal region concave, sloping abruptly to lips; lips not flared; interorbital space flat, no cranial crests; upper eyelid width 67.7–100.0 (\bar{x} = 89.9, N = 24) percent IOD; upper eyelid bearing one conical tubercle; supratympanic fold narrow, concealing uppermost edge of tympanum; tympanum prominent, round, its length 28.8–43.5 (\bar{x} = 36.0, N = 17) percent eye length in males, 30.4–46.2 (\bar{x} = 40.2, N = 8) in females; tympanum separated from eye by 1.5 tympanic diameters; tongue longer than wide, posterior border not notched, posterior one-half not adherent to floor of mouth; choanae relatively large, round not concealed by palatal shelf of maxillary arch when roof of mouth is viewed from directly above; vomerine odontophores posteromedial to choanae, low, oblique, widely separated (by distance equalling 1.5 choanal widths), bearing 2–3 teeth. Skin of dorsum smooth to finely areolate; no dorsolateral folds; discoidal folds obscure; anal opening not extended by skin flap; no ulnar tubercles or folds except for small antebrachial tubercle; palmar tubercle bifid, much larger than oval thenar tubercle; subarticular tubercles small, round, non-conical, simple; fingers bearing narrow lateral fringes, even along outer edge of palm and finger IV; all digits bearing discs on broadly dilated pads, pads round at tip; outer pads larger than inner pads; fingers long and slender.

No tubercles on knee or heel; outer edge of tarsus lacking tubercles; inner edge of tarsus bearing fold running length of tarsus and bearing 2–3 small tubercles; inner metatarsal tubercle 2–3 times as long as wide, non-compressed, 4 times size of subconical outer metatarsal tubercle; plantar surface areolate; subarticular tubercles round, elevated, non-conical, simple; toes bearing narrow lateral fringes; all toes bearing discs on dilated pads; pads of toes slightly larger than those of fingers; hind legs moderately long, shank 48.4–57.6 (\bar{x} = 52.7, N = 25) percent SVL.

Pale cream above with brown inter-orbital bar, canthal and supratympanic stripes; no facial bars; limbs not barred or there are indefinite brown bands at wrist and near knee; posterior surface of thigh pale brown; belly creamy white. KU 143510 has the face washed with brown. KU 143512 has a pale spot anterior to eye.

Color in life.—Dorsum usually pale green to dull green with no distinct markings; in some individuals dorsum tan or brown with or without brown markings; venter grayish or creamy yellow to bright yellow; vocal sac bright yellow; iris reddish bronze to reddish copper.

Measurements of holotype in mm.—SVL 19.9; shank 10.2; head width 7.4; head length 7.0; upper eyelid width 2.2; IOD 2.4; tympanum length 1.0; eye length 2.6; E-N 2.0.

Etymology.—Named for the late James A. Peters who pioneered the herpetological exploration of the Amazonian slopes and along whose trails we now search.

Distribution and ecology.—This small green *Eleutherodactylus* occurs in cloud forests at elevations of 1410–1950 m on the eastern face of the Andes in Departamento Putumayo, Colombia, and Provincia Napo, Ecuador. Five individuals referred to this species from San Agustín, Departamento Huila, Colombia, are from an elevation of 1750 m in cloud forest on the eastern slope of the Cordillera Central in the upper drainage of the Río Magdalena.

All individuals were found at night. Most were on the leaves of herbs or bushes within 1 m of the ground, but two were on leaves and one on a twig more than 1.5 m above the ground. Calling males were found in March, May, July, September, and October. The call consists of a single “peep.”

The late James A. Peters recorded the following notes on these frogs (notes 27 June 1962, specimens from 2 km SE La Bonita, Provincia Napo): “4862-80 were taken in the base of elephant ear leaves, where water collects. The lighter areas on body and legs were a golden or yellow in life; the toe and finger disks were coppery. The dorsal dark areas ranged from a chocolate brown to a light brown. They react in one of two ways to the stem being pulled down. Some hop up the stem and dive into the underbrush, while others scoot backwards down deeply into the overlapping stems, into the water, where their big eyes are visible. In life there is a distinct tho small horn over each eye and one on the snout.”

Remarks.—*E. petersi* is considered to be a northern replacement for *E. bromeliaceus* and both are considered upland replacements for the lowland *E. lacrimosus*. Both Amazonian slope species have tubercles on the upper eyelid. Based on limited data, *E. petersi* exhibits pronounced geographic variation in size (Table 4). The sample of males from the upper Pastaza trench (Baños, Río Blanco, and Yungilla) at 1600–2000 m consists of frogs as large as *E. brome-*

TABLE 4.—Variation in body size in *Eleutherodactylus petersi*.

Locality (collection)	Calling Males	Gravid Females ¹
La Bonita (JAP)	14.5-17.2(16)	19.3-22.8(2)
	16.1 ± 0.4	21.0
Río Quijos (KU) and Loreto (JAP)	16.7-19.9(14)	21.2-23.1(3)
	18.4 ± 0.6	22.0
Mera (KU)	16.9-18.0(5)	20.3-21.9(4)
	17.3 ± 0.4	21.0
Baños (JAP, UMMZ)	19.0-23.5(10)	-----
	21.4 ± 0.9	-----

¹ Each sample of females includes young (nearly mature) individuals; this fact plus small sample sizes mean that mean size estimates are probably low estimates.

liaceus (Table 2) or slope populations of *E. lacrimosus* (Table 1) but considerably larger than males of *E. petersi* from the lower reaches of the Pastaza trench (Mera, 1100 m), the vicinity of the type-locality (1410–1700 m), or the Río Chingual at La Bonita (1920 m). Although populations of *E. lacrimosus*, *E. lanthanites*, *E. nigrovittatus*, and *E. peruvianus* consist of larger frogs at higher elevations (see Tables 1 and 3) this explanation is unsuitable for *E. petersi*. The frogs from the upper Pastaza trench may represent yet another species of this complex; these frogs have larger digital pads than are seen in other specimens here assigned to *E. petersi*.

Eleutherodactylus prolatus new species

Fig. 4G

Holotype.—KU 166008, an adult female, taken 2 km SSW Río Reventador, Provincia Napo, Ecuador, 1490 m, on 6 October 1974 by William E. Duellman and John E. Simmons.

Paratypes.—KU 166009–15, collected at the type-locality.

Diagnosis.—1) skin of dorsum feebly warty, bearing H-shaped ridges on occiput, that of venter areolate; 2) tympanum prominent, its length $\frac{1}{4}$ – $\frac{2}{5}$ eye length; 3) snout acuminate in dorsal view, nearly truncate in lateral profile; canthus rostralis moderately sharp; head longer than wide; 4) upper eyelid narrower than IOD, bearing one pungent tubercle; no cranial crests; 5) vomerine odontophores prominent, oblique and oval; 6) males with vocal slits and subgular vocal sac; 7) first finger shorter than second; fingers bearing moderately large pads (II–IV); discs broader than long; 8) fingers lacking lateral fringes; 9) no ulnar tubercles; 10) heel and tarsus bearing row of conical tubercles; 11) two metatarsal tubercles, inner elongate, 8–10 times size of faint outer; no supernumerary plantar tubercles; 12) toes lacking lateral fringes and webbing; toe pads as large as those of fingers; 13) gray to brown above with cream H-

shaped occipital mark; venter cream spotted with brown; throat streaked with brown and creamy white; posterior thigh stippled with brown; 14) adults small, males 13.7–18.4 mm, females 20.8–24.1 mm SVL.

Eleutherodactylus prolatus is superficially similar to juvenile *E. rubicundus*, especially in throat pattern, but is readily distinguished in having the H-shaped occipital mark, long head, and being smaller. *Eleutherodactylus prolatus* shares the long head and several other minor features with *E. ignicolor* Lynch and Duellman, *E. trachyblepharis* (Boulenger), and *E. variabilis* Lynch. *Eleutherodactylus prolatus* has a more tuberculate skin than *E. trachyblepharis* or *E. variabilis*. *Eleutherodactylus ignicolor* has red flash colors in the groin (colorless in preservative) and lacks the tubercles on the heel.

Description.—Head narrower than body, longer than wide; head length 110.0–115.0 (\bar{x} = 111.6, N = 7) percent head width in males, 103.6–115.6 (\bar{x} = 109.0, N = 12) percent in females; head width 33.8–39.6 (\bar{x} = 36.5, N = 31) percent SVL; E–N 70.4–91.3 (\bar{x} = 80.8, N = 18) percent eye length in males, 80.0–103.3 (\bar{x} = 93.7, N = 10) percent in females; tip of snout swollen and elongated; nostrils protuberant, directed laterally; loreal region concave, sloping to lips; lips not flared; interorbital space flat, no cranial crests; upper eyelid width 82.6–126.7 (\bar{x} = 99.2, N = 26) percent IOD; upper eyelid bearing one or two conical tubercles; temporal region nearly vertical; supratympanic fold obscure or absent; tympanum distinct, higher than long, separated from eye by distance equal tympanum length, its length 24.1–37.0 (\bar{x} = 31.8, N = 18) percent eye length in males, 28.6–44.4 (\bar{x} = 35.2, N = 10) percent in females; postrictal tubercles conical as are those along margin of lower jaw; choanae small, round, not concealed by palatal shelf of maxillary arch; vomerine odontophores oblique and oval, well elevated, median and posterior to choanae, separated me-

dially by distance equal to choanal width, each odontophore one-half size of a choana, bearing a slanted row of 3-4 teeth; tongue slightly longer than wide, posterior edge feebly notched, posterior $\frac{1}{4}$ - $\frac{1}{2}$ not adherent to floor of mouth.

Skin of dorsum feebly warty, that of venter coarsely areolate; no dorsolateral folds; discoïdal fold prominent, well anterior to groin; H-shaped ridge on occiput; anal opening not extended; no obvious ulnar tubercles; small antebra-chial tubercle present; palmar tubercle bifid, larger than oval thenar tubercle; if present, supernumerary palmar tubercles low, few in number; subarticular tubercles round, low, simple; fingers lacking lateral fringes or keels; all fingers bearing broad discs; thumb lacking digital pad, those of II-IV dilated; apically round.

Tarsus bearing row of conical tubercles along outer edge; inner edge of tarsus lacking tubercles or bearing one indistinct tubercle; one conical tubercle on heel; inner metatarsal tubercle elongate (length three times width), not compressed, 8-10 times size of small, round, low outer metatarsal tubercle; plantar surface lacking supernumerary tubercles; subarticular tubercles low, flat, round; toes lacking lateral fringes of keels and webbing; all toes bearing pads (that of inner toe narrowest), with broad (broader than long) discs, rounded apically; heels of flexed hind legs overlap; heel of adpressed hind leg reaches nostril; shank 48.1-60.1 (\bar{x} = 55.4, N = 30) percent SVL.

In preservative, gray above with brown blotches, sacral chevron, 2-3 bars on flank, and cream H-shaped occipital mark; brown canthal, supratympanic, and labial markings; limb bars narrow, oblique on shank; anal triangle brown, diffuse; anterior and posterior surfaces of thighs and concealed shank stippled with brown; venter cream, spotted with brown; anterior chin white bordered posteriorly by brown bar and median gular brown streak; lateral to gular stripe

are two slanted brown bars extending onto lip.

Color in life.—Dorsum in most individuals is tan to brown (reddish brown or olive-tan in some) with dark brown to black markings and orange occipital ridges. Two individuals were green with brown marks; another was gray anteriorly and posteriorly and pale green medially. Posterior thighs brown. A few individuals have yellow flecks dorsally and a golden tint to upper lips. The venter varies from dull cream with dense brown flecking to gray, flecked or not with black. Throat dull green to brown or gray with darker streaks (cream streaks in two). Iris gray-brown.

Measurements of holotype in mm.—SVL 22.3; shank 12.6; head width 8.4; head length 8.7; upper eyelid width 2.1; IOD 2.3, tympanum length 1.0; eye length 3.0; E-N 2.8. The holotype is a gravid female.

Etymology.—Latin, meaning drawn out, in reference to the apparent elongation of the head.

Distribution and ecology.—This species is known only from lower cloud forests (1140-1490 m) on the eastern face of the Andes in Ecuador. Except for one individual found on the forest floor by day, all were on low vegetation at night; most were in ravines near streams.

Eleutherodactylus proserpens Lynch

Eleutherodactylus proserpens Lynch, 1979, Misc. Publ. Mus. Nat. Hist. Univ. Kansas 66:32 [*Holotype.*—USNM 198484, from between Sapote and Suro Rancho, Provincia Morona-Santiago, Ecuador, 2622 m].

Eleutherodactylus proserpens occurs in cloud forests at elevations of 1707 to 2622 m on the Cordillera del Condor and the Cordillera de Matanga in the Andes of southern Ecuador (Lynch, 1979a).

Eleutherodactylus pugnax Lynch

Fig. 4H

Eleutherodactylus pugnax Lynch, 1973, Bull. So. California Acad. Sci. 72:107 [*Holotype.*—KU 146466, an adult female, taken at

Salto de Agua, 2.5 km NNE Río Reventador, Provincia Napo, Ecuador, 1660 m].

Diagnosis.—1) skin of dorsum bearing flattened, ill-defined warts, flanks and venter areolate; no dorsolateral folds; 2) tympanum absent; 3) snout semicircular in dorsal view, truncate in lateral profile; canthus rostralis round; 4) upper eyelid as wide as IOD, lacking pungent tubercles; no cranial crests; 5) vomerine odontophores round, prominent; 6) males with vocal sac and slits, thumb bearing non-spinous nuptial pad; 7) first finger shorter than second; fingers bearing large pads (largest on II–IV); discs broader than long; 8) fingers bearing lateral fringes; 9) low ulnar warts present; 10) no tubercles on outer edge of tarsus or heel; inner tarsal fold along distal one-third of tarsus; 11) two metatarsal tubercles, inner oval, 5–6 times size of indistinct outer; supernumerary plantar tubercles indistinct, few in number; 12) toes bearing lateral fringes and basal webbing; webbing formula I 2–2 II 2–3⁺ III 2 1/2–4–IV 3 3/4–2 1/3 V; toe pads enlarged, slightly smaller than pads of outer fingers; 13) brown with darker markings (interorbital bar, blotches on back, facial stripes and bars, transverse limb bars); posterior surfaces of thighs brown with cream flecks; venter cream with brown flecks or spots; 14) adults moderate-sized, two males 22.1–28.0 mm, two females 30.8–33.2 mm SVL.

Eleutherodactylus pugnax is readily distinguished from all other members of the *unistrigatus* group in having toe webbing and lacking the ear. It is most similar to an undescribed species found at elevations between 1900 and 2700 m on the Pacific Andean slopes of northern Ecuador; that species has less prominent toe webbing.

Description.—See Lynch (1973b).

Color in life.—Gray-brown, dull olive-green, or yellow-tan above with brown markings; throat cream with tan flecks; venter gray with brown flecks or bluish-white flecks; iris reddish brown, olive-

brown, or pale gold with diffuse red streak.

Distribution and ecology.—The few specimens of *E. pugnax* have been at the edges of streams in cloud forest at 1660–2540 m on the eastern face of the Andes in Provincia Napo, Ecuador. Two were under rocks at the edge of a cascading stream by day. One was sitting on a rock in a stream at night and two others were on leaves of herbs at night.

Eleutherodactylus pycnodermis Lynch

Eleutherodactylus pycnodermis Lynch, 1979, Misc. Publ. Mus. Nat. Hist. Univ. Kansas 66:35 [*Holotype*.—USNM 199754, San Vicente, Provincia Morona-Santiago, Ecuador, 2805–2835 m].

Eleutherodactylus pycnodermis seems to be primarily an inhabitant of páramo and ranges down into meadows and pastures in upper cloud forests. It is known at elevations of 2652–3384 m on the Cordillera de Matanga in southern Ecuador (Lynch, 1979a).

Eleutherodactylus quaquaversus Lynch

Eleutherodactylus quaquaversus Lynch, 1974, Occas. Pap. Mus. Nat. Hist. Univ. Kansas (31):9 [*Holotype*.—KU 123745, an adult female from a series collected on the south slope Cordillera del Dué above Río Coca, Provincia Napo, Ecuador, 1150 m].

Diagnosis.—1) skin of dorsum shagreened, that of venter coarsely areolate; no dorsolateral folds; 2) tympanum concealed (or partially exposed); 3) snout subacuminate in dorsal view, rounded or weakly pointed in lateral profile; 4) upper eyelid bearing conical tubercle; upper eyelid width slightly narrower than IOD; no cranial crests; 5) vomerine odontophores triangular in outline; 6) males with subgular vocal sac and vocal slits; no nuptial pad; 7) first finger shorter than second; all fingers bearing pads and discs, largest on III–IV; 8) fingers bearing narrow lateral keels; 9) no ulnar tubercles except antebrachial; 10) tarsus bearing small tubercles on inner and outer edge; one large, conical

tubercle on heel; 11) two metatarsal tubercles, inner elongate, 4–5 times size of round outer; few supernumerary plantar tubercles; 12) toes bear narrow lateral fringes, not webbed; toe pads as large as those of outer fingers; 13) dorsum pale brown to reddish brown marked with brown chevrons, interorbital bar, and spots; never with occipital W-shaped mark; no canthal or supratympanic stripes; posterior surfaces of thighs reddish, reticulated with brown (or pigmentless); venter white, frequently spotted with brown; 14) adults moderate-sized, males 19.6–22.5 (\bar{x} = 20.7, N = 29) mm, females 24.6–31.3 (\bar{x} = 27.3, N = 20) mm SVL.

Eleutherodactylus quaquaversus is most similar to *E. frater* (Werner) and *E. ockendeni* (Boulenger) but differs from both in having the conical tubercles on the eyelid and heel and in having reticulations on the posterior surfaces of the thighs (uniformly brown in *E. frater* and *E. ockendeni*). The three species are easily recognized in that each lacks a canthal stripe.

Description.—See Lynch (1974).

Color in life.—Pale tan at night, becoming pale brown, olive-tan, or dark brown by day; markings brown; in juveniles, venter black anteriorly and yellow posteriorly (continuing onto undersides of legs); in adults, venter white to cream-bronze with gray to brown spots; lower flanks and groin white to pale pink with black flecks or pink to purplish red with white to yellow flecks; posterior surfaces of thighs are pale rose to purplish red and may bear white spots; iris silvery gray to cream without a horizontal streak.

Distribution and ecology.—Although *E. quaquaversus* is known from elevations as low as 320 m in the upper Amazon Basin in Ecuador, it reaches its greatest abundance in cloud forests between 1150 and 1830 m on the eastern face of the Ecuadorian Andes. Nearly all specimens were perched on low bushes and herbs at night.

Eleutherodactylus rubicundus (Jiménez de la Espada)

Fig. 5A

Hylodes rubicundus Jiménez de la Espada, 1875, Vert. Viaje al Pacífico . . . Batracios, plate 3, figs. 4, 4a–b [Holotype lost, type-locality unknown].

Eleutherodactylus rubicundus: Gorham, 1966, Das Tierreich, 85:99.

Diagnosis.—1) skin of dorsum coarsely tuberculate bearing vague outline of W-shaped occipital ridges, that of venter finely areolate; 2) tympanum prominent, its length $\frac{1}{2}$ eye length; 3) snout subacuminate to rounded in dorsal view, rounded in lateral profile; canthus rostralis moderately sharp, loreal region sloping gradually to lips; 4) upper eyelid broader than IOD, not bearing pungent tubercles; furrowed interorbital region in adult females; 5) vomerine odontophores prominent, triangular in outline; 6) males lacking vocal slits and sac; 7) first finger slightly longer than second; fingers long and slender, bearing large, weakly emarginate pads (III–IV); discs broader than long; 8) fingers lacking lateral keels; 9) ulnar tubercles small, subconical; 10) heel bearing elongate, conical tubercle; conical tubercles on outer edge of tarsus; 11) two metatarsal tubercles, inner elongate, 4 times size of subconical outer; several indistinct supernumerary plantar tubercles; 12) toes bearing narrow lateral fringes, no webbing; toe pads slightly smaller than those of outer fingers; 13) brown with darker brown markings above; venter cream blotched and marbled with brown; posterior thighs rich brown with cream flecks; 14) adults moderate-sized, four adult males 32.0–35.6 mm, two adult females 46.5–51.2 mm SVL.

Eleutherodactylus rubicundus is most similar to and most closely related to *E. crenunguis* Lynch of the Pacific Andean versant of central Ecuador. The two are readily distinguished in that *E. crenunguis* has a shagreened dorsum, less pungent ulnar and tarsal tubercles, flared lips, and bilobed subgular vocal sac.

Description.—Head as wide as body,

as long as wide; head width 33.9–39.7 (\bar{x} = 37.5, N = 7) percent SVL; snout subacuminate in dorsal view in males (rounded in females), rounded in lateral profile; snout long, E–N 94.5–105.9 (\bar{x} = 100.8, N = 6) percent eye length; nostrils weakly protuberant, directed laterally; loreal region weakly concave, sloping gradually to lips (slope steepest in small individuals; lips not flared; eyes large, upper eyelid width 110.0–140.0 (\bar{x} = 125.5, N = 5) percent IOD; interorbital space narrow, flat in males, weakly furrowed in adult females; temporal region nearly vertical; supratympanic fold tuberculate, not concealing tympanic annulus; tympanum prominent, higher than long, its length 32.4–40.2 (\bar{x} = 36.0, N = 6) percent eye length, separated from eye by distance equal to 1.5 tympanum lengths; postriatal tubercles prominent; choanae moderate-sized, round or slightly longer than wide, not concealed by palatal shelf of maxillary arch; vomerine odontophores meabout size of a choana, separated medially and posterior to choanae, each by distance equal to $\frac{1}{2}$ – $\frac{3}{4}$ odontophore width, triangular in outline, elevated, each bearing a weakly sloping transverse row of 4–9 blunt teeth; tongue large, a little longer than wide, posterior border feebly notched, posterior two-fifths adherent to floor of mouth.

Skin of dorsal surfaces of head and body coarsely tuberculate; one large tubercle on snout just anterior to eyes, another between eyes; upper eyelid bearing 1–2 large, non-conical tubercles; vague outline of W-shaped ridges on occiput; no other folds on dorsum; upper surfaces of limbs less tuberculate than dorsum; discoidal folds prominent, well anterior to groin; skin posterior and posterolateral to vent coarsely areolate; vent not extended in sheath; two prominent subanal tubercles; antibrachial tubercle largest in series of subconical ulnar tubercles; palmar tubercle bifid, outer lobe nearly isolated, smaller than oval thenar tubercle; supernumerary palmar tubercles prominent, those above outer

metacarpal forming an elongate tubercle, all smaller than subarticular tubercles which are round, simple, non-conical; no lateral fringes on fingers; all digits bearing discs (wider than long) on pads; dilation ratios of pads (pad width/digit width below pad) [range follows digit number, mean in parentheses] I 1.5–1.7 (1.6), II 2.1–2.3 (2.2), III 3.2–3.6 (3.5), IV 3.4–3.5 (3.5); unguinal flaps indented, pads on fingers III–IV appear emarginate, slightly on I–II.

Heel tuberculate, all tubercles round, some long, one large conical tubercle at upper edge of heel; series of 2–4 conical outer tarsal tubercles; 1–2 small inner tarsal tubercles on ill-defined tarsal ridge; outer metatarsal tubercle subconical, round to slightly longer than wide, $\frac{1}{4}$ size of elongate (length three times width), non-compressed inner metatarsal tubercle; series of conical tubercles along outer edge of foot; 1–2 round supernumerary plantar tubercles at bases of toes II–V; several low, flat, additional supernumerary plantar tubercles; subarticular tubercles longer than wide, subconical to conical, simple; toes bearing narrow lateral fringes coalescing at bases of toes into nearly indistinguishable basal web; toes bearing discs (broader than long) on dilated pads (smaller than those of fingers III–IV); unguinal flaps not notched; heels of flexed hind legs overlap broadly; heel of adpressed hind leg reaches beyond snout tip; shank 54.8–61.9 (\bar{x} = 57.8, N = 7) percent SVL.

In preservative, brown above with darker brown markings—occipital W, sacral chevron, postsacral bar, interorbital bar, canthal-supratympanic stripe, labial bars, limb bars; flanks less dark than dorsum; venter cream, blotched and marbled with brown (least distinct in groin and on lower venter); throat barred with brown; anal triangle brown posterior surfaces of thighs rich brown with cream flecks; shank bars oblique, narrower than interspaces; W-shaped occipital mark, scapular spots, and some limb bars edged with black.

Color in life.—Dorsum green or

brown variously marked with reddish brown, dark brown, olive-green, or orange; venter dull greenish yellow to grayish white or orange-tan, mottled with brown or gray; hidden surfaces of thighs dark brown to reddish salmon; iris bronze with brown or black reticulations.

Distribution and ecology.—This species has a restricted distribution in the lower part of the Pastaza trench (1080–1300 m) and to the north in the Cordillera del Dué (1150 m). All individuals have been found on herbs, bushes, or low (up to 2 m) limbs of trees at night in cloud forest.

Remarks.—Lynch and Schwartz (1972) summarized the characteristics evident in Jiménez de la Espada's (1875) illustration but deferred to associate the name with any known population of *Eleutherodactylus*. The arrangement of tubercles on the body and limbs of *E. rubicundus* is reasonably congruent with that seen in *E. appendiculatus* (Werner), *E. calcaratus* (Boulenger), *E. crucifer* (Boulenger), *E. galdi* (Jiménez de la Espada), and *E. orcostalis* Rivero, but on the basis of color patterns and proportions, none of these can be considered as identical with *E. rubicundus* (and all are associated with distinctive frog populations). The frogs here associated with *E. rubicundus* from the lower Andean slopes in eastern Ecuador are not separable from the illustrations of the frog Jiménez de la Espada (1875) called *Hylodes rubicundus*. This tenuous argument is joined by the equally tenuous one that several of the species reported by Jiménez de la Espada (1875) are found together in the upper Amazon Basin in central Ecuador.

Lynch (1976b, d) placed *E. crenunguis* in the *fitzingeri* group of *Eleutherodactylus*. *Eleutherodactylus rubicundus* is without doubt closely allied to *E. crenunguis* but its association with the *fitzingeri* group would strain definition of the group. The indented unguial flap

of the digits of the two species are dissimilar to the apically rounded flaps seen in members of the *fitzingeri* group. In order to reflect the similarities of *E. crenunguis* and *E. rubicundus* and to preserve the integrity of the *fitzingeri* group, *E. crenunguis* and *E. rubicundus* are here assigned to an assembly within the *unistrigatus* group. This arrangement is not entirely satisfactory, but until other allies are identified, it seems to be the best course. This assembly is defined as follows: skin of venter smooth or feebly areolate; first finger longer than second; tympanum prominent, annulus not concealed; vomerine odontophores prominent, triangular in outline; head narrow (HW/SVL .339–.418); low cranial crests in large females; interorbital space narrow; unguial flap indented (at least on fingers); digits bearing pads; toes not webbed.

Lynch (1976d) noted that *E. cruentus* (Peters) and especially *E. latidiscus* (Boulenger), both members of the *unistrigatus* group, resembled *E. crenunguis* in having flared lips and indented unguial flaps (and digital pads) but that the *unistrigatus* group species have areolate skin on the venter and the thumb is shorter than the second finger. The Amazonian slope species, *E. rubicundus*, bridges much of the apparent gap. With *E. cremnobates*, the species form a series as follows: *crenunguis* — *rubicundus* — *cremnobates* — *latidiscus* — *cruentus*. The series will be expanded when the fauna of the Pacific versant of Ecuador is more completely described.

Eleutherodactylus spinosus Lynch

Eleutherodactylus spinosus Lynch, 1979, Misc. Publ. Mus. Nat. Hist. Univ. Kansas 66:43 [Holotype.—USNM 199891, Sapote, Provincia Morona-Santiago, Ecuador, 2470 m].

Eleutherodactylus spinosus occurs in cloud forests at elevations of 1707–2835 m on the Cordilleras del Condor and Matanga in southern Ecuador (Lynch, 1979a).

Eleutherodactylus trachyblepharis

(Boulenger)

Fig. 5B

Hylodes trachyblepharis Boulenger, 1918, Ann. Mag. Nat. Hist. (9) 2:429 [Syntypes.—BM 1912.11.1.58–60/RR 1947.2.17.2–4, collected at El Topo, Provincia Tungurahua, Ecuador, 4200 feet].

Eleutherodactylus trachyblepharis: Peters, 1955, Rev. Ecuat. Ent. Par. 2:349.

Diagnosis.—1) skin of dorsum smooth or with low warts on posterior back, no dorsolateral folds, that of venter coarsely areolate; 2) tympanum partially concealed beneath skin, its length $\frac{1}{2}$ – $\frac{2}{3}$ eye length; 3) snout acuminate in dorsal view, rounded in lateral profile, swollen; canthus rostralis distinct; 4) upper eyelid narrower than IOD, lacking tubercles; no cranial crests; 5) vomerine odontophores very low, oblique; 6) males lack vocal sac and slits; no nuptial pad; 7) first finger shorter than second; pads enlarged, smaller than tympanum; discs broader than long; 8) fingers lack lateral fringes; 9) no ulnar tubercles; 10) no tubercles on heel or tarsus; 11) two metatarsal tubercles, inner oval, 3–4 times size of round outer; 2–4 indistinct supernumerary plantar tubercles; 12) toes lack lateral fringes, no webbing; toe pads equal to or slightly larger than those of outer fingers; 13) tan above with sparse brown markings; venter cream, stippled with brown, concealed surfaces of thighs brown; 14) adults minute, males 12.1–15.8 (\bar{x} = 13.8, N = 20) mm, females 15.8–19.2 (\bar{x} = 17.2, N = 19) mm SVL.

Eleutherodactylus trachyblepharis is the smallest species of the genus found in South America. It is probably most closely related to the slightly larger *E. ignicolor* Lynch and Duellman, *E. prolatus* Lynch and Duellman, and *E. variabilis* Lynch; all four have heads that are longer than wide. *Eleutherodactylus trachyblepharis* lacks a pattern on the throat (unlike *E. ignicolor* and *E. prolatus*) and venter and groin (unlike *E. variabilis*). *Eleutherodactylus ignicolor* and *E. prolatus* have tubercles on the

outer edge of the tarsus and have larger digital pads. The pads of *E. variabilis* are truncate unlike the round pads of *E. trachyblepharis*.

Description.—Head narrower than body; head longer than wide [head length 111.4–117.8 (\bar{x} = 114.9, N = 9) percent head width in males, 101.7–113.6 (\bar{x} = 106.8, N = 7) in females]; head width 32.9–37.0 (\bar{x} = 34.3, N = 16) percent SVL; tip of snout swollen, accentuating head length; E–N 72.7–88.2 (\bar{x} = 77.7, N = 9) percent eye length in males, 78.3–90.5 (\bar{x} = 86.1, N = 7), in females; nostrils weakly protuberant, directed laterally; loreal region nearly flat, sloping abruptly to lips; lips not flared; upper eyelid 73.5–93.8 (\bar{x} = 81.6, N = 9) percent IOD in males, 77.8–94.4 (\bar{x} = 89.0, N = 7) in females, lacking tubercles; no cranial crests; supratympanic fold obsolete; tympanum partially concealed beneath skin, anterior and ventral edges of tympanic annulus distinct; tympanum round in males, higher than long in females, separated from eye by half its length in males, its length in females; tympanum length 33.3–42.9 (\bar{x} = 37.8, N = 9) percent eye length in males, 26.1–38.1 (\bar{x} = 33.4, N = 7) in females; postrictal tubercles not evident; choanae relatively small, longer than wide, near edge of palate; vomerine odontophores absent in some adults, when present, median and posterior to choanae, separated medially by distance equal 1.5–2 times odontophore width, oblique, about size of a choana, bearing 0–4 teeth in slanted row; tongue longer than wide, posterior border feebly notched, posterior half not adherent to floor of mouth.

Skin of dorsum smooth or with vague flat warts on lower back, flanks smooth, no dorsolateral folds; discoidal folds well anterior to groin; no anal sheath or anal warts; no ulnar tubercles; palmar tubercle bifid, 1.5 times size of oval thenar tubercle; supernumerary palmar tubercles low, numerous; subarticular tubercle round, non-conical; fingers lack lateral fringe or keel; discs nearly round but wider than long; pads apically rounded,

largest on III–IV (1.5–2 times width of digit), all expanded, all smaller than tympanum.

No tubercles on heel or tarsus; inner metatarsal tubercle low, oval (length 2.5 times width); outer metatarsal tubercle round, pungent, $\frac{1}{8}$ – $\frac{1}{4}$ size of inner; supernumerary tubercles flat, at bases of toes II–IV (also few on plantar surface proper), large (nearly as large as subarticular tubercles which are round, pungent); no lateral fringe or keel on toes; no webbing; pads on toes about same size as those of outer fingers; heels broadly overlap when hind legs are flexed; heel of adpressed hind leg reaches to between eye and nostril; shank 49.0–55.8 (\bar{x} = 52.9, N = 16) percent SVL.

In preservative, tan or pale brown above with brown interorbital bar, dark occipital W, scapular spots, diverging bars from sacrum to flank, canthal-supratympanic stripe, labial bars, limb bars; limb bars about as wide as interspaces, oblique on shank; anal triangle dark brown; cream or tan line above vent; posterior surfaces of thighs uniform brown; throat and venter cream peppered with brown.

Color in life.—Dorsal surfaces pale yellow to light brown or reddish brown (sometimes with pale green wash) with brown and/or black markings; flanks yellow with brown area behind insertion of arm; occasional examples have orange wash in groin; anal triangle light to dark brown, cream or white bar above vent; posterior surfaces of thigh gray to brown; venter off-white to gray, throat yellow; iris pale gray with reddish brown; horizontal streak (iris in some individuals has red wash).

Measurements of adult male and female in mm.—(KU 120200 and 120203, respectively): SVL 14.9, 17.5; shank 7.3, 9.0; head width 4.9, 5.9; head length 5.7, 6.7; upper eyelid width 1.4, 1.4; IOD 1.7, 1.6; tympanum length 0.8, 0.8; eye length 2.2, 2.3; E–N, 1.7, 1.8.

Distribution and ecology.—Most specimens of *E. trachyblepharis* are from the

valley of the Río Pastaza (950–1250 m) where special efforts were made to secure specimens. The other records are from low elevations (320–530 m) in Provincia Pastaza. The presently known distribution (low to moderate elevations along the Río Pastaza) may be real in view of the occurrence of a similar species (*E. prolatus*) at slightly higher elevations to the north or may be an artifact of most collectors failing to scrutinize the low herbaceous layer of the forest floor at night and the reluctance of many collectors to pick up what appear to be juvenile *Eleutherodactylus*.

Most specimens have been found on small herbs 10–30 cm above the ground in primary and secondary forest. KU 120254 was found in a recently drained swamp in a cleared area at Sarayacu. Although *E. trachyblepharis* lacks vocal slits and vocal sac, males call. KU 120199–200 were collected as they were calling on vegetation along a small forested stream at Abitagua. The call is a “sharp chirp-like click, one every 3–5 seconds.”

The ovarian complement is small in so small a frog. KU 120203 has three large ovarian eggs as well as many smaller eggs. The left ovary contains two large eggs, 1.8×1.8 and 1.8×2.3 mm; the right ovary contains one large egg, 1.8×2.5 mm.

Eleutherodactylus trepidotus Lynch

Fig. 5C

Paludicola festae Peracca, 1904, Boll. Mus. Zool. Anat. Comp. 19:32 [*Lectoholotype*.—MSNT 820, an adult female from Papallacta, Provincia Napo, Ecuador; lectoholotype designated by Lynch, 1975c:31; preoccupied in *Eleutherodactylus* by *Hylodes festae* Peracca (= *E. galdi*, *vide* Lynch, 1974)].

Eleutherodactylus trepidotus Lynch, 1968, Herpetologica 24:295 [*Holotype*.—USNM 164399, an adult female from 1 km W Papallacta, Provincia Napo, Ecuador, 3155 m].

Diagnosis.—1) skin of dorsal surfaces smooth with small pointed warts and short ridges and folds, that of venter

coarsely areolate; no dorsolateral folds; 2) tympanum prominent, round, its length $\frac{2}{3}$ eye length; 3) snout rounded in dorsal and lateral profiles; canthus rostralis rounded; 4) upper eyelid much narrower than IOD; no pungent tubercles on eyelid; no cranial crests; 5) vomerine odontophores low, oblique; 6) males with vocal slits and subgular vocal sac, no nuptial pads; 7) first finger shorter than second; digits bearing long discs (length equal width), lacking pads; 8) fingers lack lateral fringes; 9) no ulnar tubercles; 10) no tubercles on heel or outer edge of tarsus; no supernumerary plantar tubercles; 11) two metatarsal tubercles, inner oval, twice as large as round outer; 12) toes bearing lateral keels, no web; toes bearing narrow pads; 13) dorsum dark brown to black; facial markings distinct; flanks and venter black with pale cream or white spots (spots red in life); 14) adults small, males 14.4–21.3 (\bar{x} = 16.9, N = 5) mm, females 17.3–25.5 (\bar{x} = 21.2, N = 21) mm SVL.

Eleutherodactylus trepidotus is distinguished from most species of the *unistrigatus* group by virtue of its lack of digital pads. None of the other species lacking pads have dark venters with pale spots. *Eleutherodactylus trepidotus* is most frequently confused with specimens of the disc-less genus *Phrynopus*, but all species of *Phrynopus* in Ecuador have digits that appear pointed without magnification whereas those of *E. trepidotus* appear to be round. *Eleutherodactylus elassodiscus* also has narrow digits, but the skin of the venter is smooth and the first finger longer than the second.

Description.—See Lynch (1968b).

Color in life.—Dorsum brown washed with green; dorsal markings dark green, dark brown, or black; venter brown to black; spots on throat white to yellow; those on venter and in groin white with pale red centers to red; iris gray-brown.

Distribution and ecology.—*Eleutherodactylus trepidotus* is known in páramo and subpáramo habitats from the region of Nevado Cayambe south to the

Llanganti mountains (N side of Pastaza valley) at elevations between 2360 and 3650 m. All individuals have been taken by day beneath rocks or logs in pastures or páramos. Males are taken infrequently.

Eleutherodactylus unistrigatus (Günther)

Hylodes unistrigatus Günther 1859, Proc. Zool. Soc. London, 1859:416 [*Syntypes*.—BM 60.6.16.97–98, 60.6.16.105/RR 1947.2.17. 7–9, collected in western Ecuador by Mr. Fraser].

Phyllobates equatorialis Barbour, 1908, Bull. Mus. Comp. Zool. 51:320 [*Cotypes*.—MCZ 2261, collected at "Equator"].

Eleutherodactylus unistrigatus: Barbour and Noble, 1920, Bull. Mus. Comp. Zool. 63: 401.

Eleutherodactylus unistrigatus [*unistrigatus*]: Cochran, 1948, Amer. Mus. Novitat. (1375):1.

Diagnosis.—1) skin of dorsum smooth to shagreened with small scattered warts, flanks bearing flattened warts, that of venter coarsely areolate; no dorsolateral folds; 2) tympanum distinct, its length about half eye length; 3) snout round or subovoid in dorsal view, round in lateral profile; canthus rostralis rounded; 4) upper eyelid much narrower than IOD; upper eyelid not bearing pungent tubercles; no cranial crests; 5) vomerine odontophores oblique, indistinct in small individuals; 6) males with vocal slits and subgular vocal sac; no nuptial pads; 7) first finger shorter than second; enlarged pads on fingers II–IV, discs broad; 8) fingers lack lateral fringes; 9) ulnar tubercles poorly defined; 10) heel and tarsus lacking tubercles except for poorly defined inner tarsal tubercle; 11) two metatarsal tubercles, inner oval, 6–7 times size elongate outer metatarsal tubercle; supernumerary plantar tubercles few in number; 12) toes bearing narrow lateral fringes, not webbed; toe pads as large as those of outer fingers; 13) pattern polymorphic; most individuals cream, tan, or brown with brown or black interorbital bar, dorsal chevrons, suprainguinal bar, slanted bars on flanks, canthal-supratympanic stripe, labial bars;

limbs marbled with brown (bars indistinct); posterior surfaces of thighs and groin cream with brown marbling or not; venter cream; throat of male yellow, that of female cream peppered with brown; 14) adults small, males 15.5–23.4 (\bar{x} = 8.8, N = 26) mm, females 23.3–30.8 (\bar{x} = 25.4, N = 45) mm SVL (Amazonian slopes only).

Eleutherodactylus unistrigatus is closely related to several species found at moderately high elevations in Colombia and Ecuador [*E. bogotensis* (Peters), *E. cajamarcensis* Barbour and Noble, *E. coeruleus* (Andersson), *E. erythropleurus* (Boulenger), *E. lehmanni* (Boettger), *E. orcesi* Lynch, *E. pastazensis* Andersson, *E. riveti* (Despax), and *E. thymelensis* Lynch]. *Eleutherodactylus unistrigatus* is most easily recognized because it is a small tan, squat-bodied frog having brown or black chevrons and bars on the dorsal surfaces. It is not separable from *E. coeruleus* (Andersson) or *E. lehmanni* (Boettger), but placing those taxa in synonymy is deferred to Lynch's forthcoming paper on the frogs of the genus found in the northern Andes.

Description.—The only usable descriptions are those by Andersson (1945) for *Syrrhophus coeruleus* and Cochran and Goin (1970) for *Eleutherodactylus lehmanni*. Considerable variation is evident among highland populations, and that variation is evident when comparing the two descriptions.

Color in life.—Dorsum creamy tan, yellow, orange brown, or brown with brown to black markings; middorsal stripe (if present) yellow; venter white to cream; throat yellow in males, dirty cream in females; posterior surfaces of thighs pale fuscous brown; iris bright copper brown above, same or reddish brown below, usually with reddish brown horizontal streak.

Distribution and ecology.—Through most of its distributional area, *E. unistrigatus* is a frog of high altitude grasslands and *Eucalyptus* groves (2300–3200 m), occurring primarily in the inter-Andean

hoyas from Pasto in southern Colombia south to Riobamba in central Ecuador. *Eleutherodactylus unistrigatus* also occurs on the Andean slopes. Presumably isolated populations are known from the vicinity of Mindo and Nono (Provincia Pichincha, Ecuador, 1500–2500 m) and Pilaló (Provincia Cotopaxi, Ecuador, 2580 m) on the Pacific slopes. Similar populations are known from the Amazonian slopes (Colón, Departamento Putumayo, Colombia, 2200 m; El Carmelo to Santa Bárbara, Provincia Napo, Ecuador, 2600–2800 m; and Baños, Provincia Tungurahua, Ecuador, 1800 m). The Baños population is contiguous with those populations found along the Ríos Chambo and Patate (and their tributaries) between Latacunga and Riobamba.

By day individuals are found beneath rocks, dirt clods, wood, bricks, paper, or under the cover of grass. At night, during December through March, males are actively calling on low vegetation (herbs within one meter of the ground). The call is a “quonk,” sometimes given in a series of 5–6 notes. Egg masses are deposited beneath rocks or dirt clods and require 39 days to hatch (Nina and del Pino, 1977). Breeding is seasonal (December through March). During the non-breeding season, males do not call, but frogs do venture from beneath cover at night to forage for insects. Circumstantial evidence suggests that both sexes mature in a single year.

Eleutherodactylus ventrimarmoratus (Boulenger)

Hylodes ventrimarmoratus Boulenger, 1912, Ann. Mag. Nat. Hist. (8)10:187 [*Syntypes*.—BM 1911.1.1.51–53/RR 1947.2.15.74–76, from El Topo, Provincia Tungurahua, Ecuador, 1280 m, collected by M. G. Palmer, and BM 1911.12.12.77/RR 1947.2.15.73, from Chanchamayo, Departamento Junín, Perú, collected by G. Shunke].

Eleutherodactylus ventricittatus Andersson, 1945, Ark. Zool. 37A:33 [*Holotype*.—NHRM (not examined), from Ambitagua (= Abituagua), Río Pastaza, Provincia Tungurahua or Pastaza, Ecuador, collected

by W. Clarke-Macintyre in September 1937]. New synonymy.

Eleutherodactylus ventrimarmoratus: Andersson, 1945, Ark. Zool. 37A:30.

Diagnosis.—1) skin of dorsum, flanks, and limbs tuberculate, that of venter aerolate; no dorsolateral folds; 2) tympanum concealed; 3) snout rounded in dorsal and lateral profiles; canthus rostralis rounded; 4) interorbital space broader than upper eyelid; upper eyelid lacking enlarged tubercles; no cranial crests; 5) vomerine odontophores triangular in outline; 6) males lacking vocal sac, vocal slits, and nuptial pads; 7) first finger shorter than second; pads large, largest on III–IV, not emarginate; 8) fingers bearing narrow lateral fringes; 9) ulnar tubercles present; 10) no tubercles on heel or outer edge of tarsus; fold on inner edge of distal one-half of tarsus; 11) two metatarsal tubercles, inner oval, six times size of round outer; supernumerary plantar tubercles not pungent; 12) toes bearing lateral fringes, no web; toe pads large but smaller than those of outer fingers; 13) brown above with diffuse gray flecks or vermiculation; flanks, anterior and posterior surfaces of thighs, and concealed shank bearing black spots or bars on colorless background; belly white, spotted or marbled with black; throat cream with pale brown marbling; 14) adults moderate-sized, males 17.8–25.5 (\bar{x} = 21.8, N = 8), females 33.3–43.8 (\bar{x} = 36.9, N = 9) mm SVL.

The pattern on the venter and concealed surfaces of the limbs precludes confusion of *E. ventrimarmoratus* with any other species. *Eleutherodactylus altamazonicus* Barbour and Dunn has similar markings in the groin and on the concealed surfaces of the limbs but does not have bold marbling on the venter and is smaller (males 14.4–23.1 mm, females 23.6–33.9 mm SVL). *Eleutherodactylus diadematus* (Jiménez de la Espada) is slightly larger (males 21.4–27.4 mm, females 35.4–44.5 mm SVL), has diffuse marbling on the venter and concealed surfaces of the limbs, and tuber-

culate skin, but has a prominent tympanum.

Description.—See Andersson's (1945) description of *E. ventrivittatus*.

Color in life.—Rich brown above with faint black markings edged with white flecks; flanks, anterior and posterior surfaces of thighs, concealed shank, and venter black and white; throat and undersurfaces of limbs red; iris pale gold.

Distribution and ecology.—*E. ventrimarmoratus* ranges from below 100 m (western Brasil) to 1740 m (Río Azuela, Provincia Napo, Ecuador). Its geographic distribution is from the cloud forests in northern Ecuador and the rainforests in western Brasil south to southern Perú. Specimens have been found on low vegetation at night and in a rotten log in swamp forest by day.

Remarks.—Lutz and Kloss (1952) suggested that *E. ventrimarmoratus* and *E. ventrivittatus* are synonymous. Andersson's (1945) description and figures of *E. ventrivittatus* are in agreement with the cotypes of *E. ventrimarmoratus*. Andersson separated his specimens from *E. ventrimarmoratus* on the basis of slight proportional differences, tongue shape, and skin texture. The difference in skin texture may well be due to preservation. The coloration, body size, concealed tympanum, digit pad size, and proportions of *E. ventrivittatus* are in agreement with *E. ventrimarmoratus* and the two are here proposed as synonyms.

Eleutherodactylus w-nigrum (Boettger)

Fig. 5D

Hylodes w-nigrum Boettger, 1892, Ber. Senck. Naturf. Ges., 1892:28 [*Holotype*.—SMF 3804, taken at Zurucuchu, approximately 15 km W Cuenca, Provincia Azuay, Ecuador, 3500 m, in 1890 by C. F. Lehmann].

Hylodes buergeri Werner, 1899, Verh. Zool.-Bot. Ges. Wien 49:476 [*Syntype*.—BM 1900.2.7.4/1947.2.15.71, Alto de Sibaté near Bogotá and Fusagasugá, Departamento Cundinamarca, Colombia. (This may be the only surviving syntype)].

Eleutherodactylus buergeri: Dunn, 1944, Rev. Acad. Colombiana Cienc. Exacta Fis. Nat. 6:73.

Eleutherodactylus w-nigrum: Peters, 1955, Rev. Ecuat. Ent. Par. 2:337; Cochran and Goin, 1970, Bull. U.S. Natl. Mus. (288):395.

Diagnosis.—1) skin of dorsum shagreened with granules and warts on upper flanks, that of venter smooth; no dorsolateral folds; 2) tympanum prominent, its length 35–52 percent eye length; 3) snout rounded or ovoid in dorsal view, round in lateral profile; canthus rostralis sharp; 4) upper eyelid width usually slight less than IOD; no pungent tubercles on eyelid; no cranial crests; 5) vomerine odontophores prominent, triangular in outline; 6) males with vocal slits and subgular vocal sac, white non-spinous nuptial pads; 7) first finger longer than second; all bearing broad discs on pads, pads largest on fingers III–IV; 8) fingers bearing lateral fringes; 9) ulnar tubercles indistinct or absent; 10) heel and tarsus lacking pungent tubercles; 11) two metatarsal tubercles, inner elongate, 6–8 times size of round outer; supernumerary plantar tubercles few or absent; 12) toes bearing lateral fringes, no webbing; pads of toes as large as those of outer fingers; 13) dorsum tan to brown with brown interorbital bar, occipital W, sacral chevron; flanks bearing dark brown to black spots; canthal-supratympanic stripe and labial bars prominent; posterior surfaces of thighs tan with brown to black spots or reticulations; groin spotted or marbled; venter cream to yellow with gray to brown spots; 14) adults large, males 29.3–46.8 (\bar{x} = 34.2, N = 32) mm, females 44.4–56.6 (\bar{x} = 49.9, N = 15) mm SVL (Amazonian slopes of southern Colombia and northern Ecuador only).

Eleutherodactylus w-nigrum is most easily recognized by virtue of having round dark spots on the flank. Round spots occur on the posterior surfaces of the thighs in the populations on the Amazonian Andean slopes. Casual inspection of the frog allows it to be confused with most members of the *fitzingeri* group. For example, Cochran and Goin (1970) reported examples of *E. w-nigrum* as *E. brederi*, *E. conspicillatus*,

and *E. longirostris*, as well as *E. w-nigrum*. Some of the examples of *Hylodes conspicillatus* reported by Boulenger (1882) are *E. w-nigrum*, and those misidentifications probably contributed to much of the confusion of the identity of *E. conspicillatus*. *Eleutherodactylus w-nigrum* is probably most closely related to *E. lymani* Barbour and Noble, from which it differs in lacking an inner tarsal fold.

Description.—See Cochran and Goin (1970).

Color in life.—Dorsum light brown to brown (sometimes becoming rusty brown above) with brown markings edged with cream; venter white, cream, or yellow (yellow in juveniles and most males); groin, anterior and posterior surfaces of thighs, and concealed shank yellow with black markings; iris bright yellow-bronze above, reddish bronze below, usually with reddish horizontal streak, reticulated with black. The pale areas on the concealed limbs and flanks are white in adults in populations from the Amazonian slopes.

Distribution and ecology.—*Eleutherodactylus w-nigrum* occurs in lower montane and cloud forests between 800 and 3300 m on both the Pacific and Amazonian slopes in Colombia and Ecuador. In Colombia, *E. w-nigrum* ranges as far north as the Medellin Valley; in Ecuador it ranges south to provincias El Oro and Zamora-Chinchiipe. By day specimens are found beneath logs, rocks, or in dead vegetation. At night frogs are especially active along streams, but may be found in forests adjacent to streams. Adult females are seldom encountered very far from streams, but young individuals and males may be extremely abundant along the forest edge (such as a road cut). Observing 40 to 50 individuals in a night is not uncommon; up to 250 individuals have been observed in a four-hour period in cloud forest.

Breeding occurs in January to April; young frogs are abundant in May to July but have disappeared by December. The call of *E. w-nigrum* is very much

like that of many *Gastrotheca*—"braaack, bonk, bonk, bonk, bonk."

Frogs from the Amazonian versant of southern Ecuador are significantly larger than those from northern Ecuador (see Tables 1 and 2). Those from northern

Ecuador are approximately the same size as frogs from northern, central, and southern Colombia whereas those from southern Ecuador (Amazonian versant) are as large as *E. w-nigrum* from the Pacific versant of northern Ecuador.

RELATIONSHIPS OF THE FAUNA

The 47 species (including two species not treated above, *E. buckleyi* and an undescribed species confused with *E. vertebralis*, belong to four species groups as recognized by Lynch (1976b) and listed below.

I. *biporcatus* group: *E. cornutus* is closely related to *E. cerastes* found at comparable altitudes on the Pacific versant of Colombia and Ecuador; three other species occur in trans-Andean South America and Central America (*biporcatus*, *bufoniformis*, and *necerus*).

II. *discoidalis* group: *E. dolops* and *E. elassodiscus* occur on the Amazonian versant as does *E. nigrovittatus*; the latter also is distributed into the Amazon Basin. One species of the group (*E. mantipus*) occurs on the Pacific versant of the Cordillera Occidental in Colombia; two occur on the Amazonian versant in southern Perú and Bolivia (*E. crucialis* and *E. grandulosus*), and one in the mountains of northern Argentina (*E. discoidalis*).

III. *fitzingeri* group: *E. condor*, *E. lanthanites*, *E. peruvianus*, and *E. w-nigrum* occur on the Amazonian versant but only *E. condor* is endemic. *Eleutherodactylus w-nigrum* is widely distributed in cloud forests in Colombia and Ecuador and not closely related to the other three (its closest allies include *E. actites* and *E. lymani*; *E. lanthanites* and *E. peruvianus* are broadly distributed over the Amazonian lowlands where they are rarely sympatric; on the Amazonian slopes they do not co-occur).

IV. *unistrigatus* group: The remaining 39 species belong to the largest species group of the genus (Lynch, 1976b), including well over 100 species. Lynch (1979a) suggested that the 18 species

of the *unistrigatus* group in southern Andean Ecuador were members of eight or nine intragroup assemblies. Some of those 18 species are members of the Amazonian slope fauna. Expanding that earlier summary of apparent relationships to the Amazonian slope fauna requires 16 intragroup units:

1. *acuminatus* assembly: *atratus* and *inusitatus* on the Amazonian slopes seem most closely related to *acuminatus* of the Amazon Basin.

2. *celator* assembly: *colodactylus* and *proserpens* on the Amazonian slopes seem most closely related to *celator* of the upper cloud forests of the Pacific versant of Ecuador.

3. *crucifer* assembly: *chloronotus* and *incanus* on the Amazonian slopes appear to be closely related, and *cryptomelas* may be allied to these species; the assembly is represented on the Pacific lowlands and slopes of Colombia and Ecuador by *E. calcaratus* and *E. crucifer*, respectively.

4. *curtipes* assembly: *buckleyi* invades the upper edge of cloud forest on the northern Amazonian slopes but is primarily a frog of the páramo, as are the closely related *E. cryophilus* and *E. curtipes*. A second series of species includes *trepidotus* (invading upper cloud forests on the Amazonian slopes), a páramo frog, as are the related *ginesi*, *myersi*, and *nicefori*.

5. *devillei* assembly: *devillei* occurs in upper cloud forests in the Papallacta Valley, an undescribed species (currently confused with *vertebralis*) occurs in similar habitats as well as páramo in the headwaters of the Río Chingual; the closest allies of these two species are *vertebralis* (cloud forests on the Pacific

versant of northern Ecuador) and another undescribed species from cloud forests on the Pacific versant of central Ecuador.

6. *diadematus* assembly: *incomptus* and *ventrimarmoratus* of the Amazonian slopes are allied to lowland species *altamazonicus*, *carvalhoi*, *croceinguinis*, *diadematus*, *martiae*, and *platydactylus* (the last occurs on the Amazonian slope in southern Perú).

7. *frater* assembly: *quaquaversus* occurs in low cloud forests on the Amazonian slopes; its allies are lowland forest frogs—*frater* in the Chocó and *ockendeni* in the upper Amazon Basin.

8. *glandulosus* assembly: *acerus*, *glandulosus*, *leucopus*, and *lividus* from upper cloud forests on the Amazonian slopes of northern Ecuador and adjacent Colombia; *percultus* from subpáramo of southern Ecuador may be closely related.

9. *lacrimosus* assembly: *bromeliaceus* and *petersi* on the Amazonian slopes of Ecuador are allied to *lacrimosus* (Amazonian Basin) and *mendax* (slopes and lowlands in southern Perú).

10. *nigrogriseus* assembly: *eriphus*, *nigrogriseus*, and *spinus* on the Amazonian slopes in Ecuador.

11. *pugnax* assembly: *pugnax* on the Amazonian slopes of northern Ecuador is closely related to an undescribed species from upper cloud forests on the Pacific versant of northern Ecuador.

12. *pyrrhomerus* assembly: *gladiator* (Papallacta Valley), *leoni* (Río Chingual and Pacific cloud forests of northern Ecuador), and *pyrrhomerus* (high cloud forests on Pacific versant in central Ecuador; the distribution of this assembly parallels that of the *devillei* assembly, except that one species (*leoni*) occurs on both Amazonian and Pacific slopes of the Andes).

13. *rubicundus* assembly: *rubicundus* (low cloud forests on the Amazonian slopes) is closely related to *crenunguis* and an undescribed species (low cloud forests on the Pacific versant of northern Ecuador); *cremnobates* (low cloud forests on the Amazonian slopes) is related

to *latidiscus* and more remotely to *cruentus* (both from lowlands and lower cloud forests) of the Chocó.

14. *surdus* assembly: *baryecus* (high cloud forests of the Amazonian slopes in southern Ecuador) is related to *surdus* (high cloud forests on the Pacific versant of the north and central Ecuador).

15. *trachyblepharis* assembly: *ignicolor*, *prolatus*, and *trachyblepharis* from the cloud forests on the Amazonian slopes of Ecuador are related to *variabilis* (Amazonian lowlands); *galdi* (Amazonian slopes in Ecuador) is apparently allied to this group.

16. *unistrigatus* assembly: this assembly includes two series; the first includes *pastazensis* and *unistrigatus* found in upper cloud forests on the Amazonian slopes as well as *bogotensis*, *erythropleurus*, and *lynchi* from Colombia and *cajamaricensis* and *versicolor* from southern Ecuador; the second series includes primarily páramo frogs (*balionotus*, *orcesi*, *pyncodermis*, *riveti*, *ruidus*, and *thymelensis*), but *pyncodermis* invades upper cloud forests on the Amazonian slope in southern Ecuador, and *ruidus* is a cloud forest frog on the Pacific versant in southern Ecuador.

The members of the *curtipes* and *unistrigatus* assemblies are primarily frogs distributed above tree-line (altitudinal range 1800 to at least 4100 m). Only *E. erythropleurus*, *E. pastazensis*, and *E. ruidus* are restricted to cloud forests, but the limits of the *unistrigatus* assembly remain to be established on the Pacific versant and in Colombia.

The members of the *celator*, *crucifer*, *devillei*, *glandulosus*, *nigrogriseus*, *pugnax*, *pyrrhomerus*, and *surdus* assemblies are frogs of cloud forests. Only *E. calcaratus* (*crucifer* assembly) invades lowland forest. At present, only the *glandulosus* and *nigrogriseus* assemblies are endemic to the Amazonian slope cloud forests; representatives of the other six assemblies occur on both Amazonian and Pacific slopes, but the absence of the *glandulosus* and *nigrogriseus* assemblies

from the Pacific slopes is probably due to incomplete study of the Pacific slope fauna.

Frogs of the *rubicundus* assembly include one series of species found in very low cloud forests (below 1500 m) on both Amazonian and Pacific slopes, as well as a second series having one species in low cloud forests on the Amazonian versant and a pair of frogs in low cloud forests and lowland rainforests on the Pacific versant.

Five assemblies (in addition to the *rubicundus* assembly) occur in cloud forests, as well as lowland forests (*acuminatus*, *diadematus*, *frater*, *lucrosus*, and *trachylepharis* assemblies). The frogs of the *acuminatus*, *diadematus*, *lucrosus*, and *trachylepharis* assemblies occur in the Amazon lowlands, as

well as in the cloud forest of the Amazonian slopes, whereas frogs of the *frater* assembly include one in the trans-Andean lowlands (*frater*), one in the lowlands of the upper Amazon Basin (*ockendeni*), and one in lower cloud forests on the Amazonian slopes in Ecuador (*quaquaversus*).

Of the 71 species included in these 16 units, only 12 occur in páramo and subpáramo (all species in the *curtipes* and *unistrigatus* assemblies) and only 15 occur in lowland forests (representatives of 6 assemblies). The majority (44) are cloud forest animals (1000–3000 m) confirming Lynch's (1979a) observation that most species in southern Ecuador (and now the Amazonian slopes as well) have their closest allies in adjacent (or the same altitudinal) strata.

DISTRIBUTION AND ECOLOGY

The delimitation of distributions of species and recognition of communities frequently is a difficult task in regions of high relief and complex topography. The Amazonian slope of the Andes in Ecuador is no exception. Prior to the analysis of the distribution and the discussion of the communities we provide the reader with a description of the region and a physiographic map showing localities where specimens were collected (Fig. 6).

DESCRIPTION OF REGION

Viewed from the lowlands of the upper Amazon Basin, the Cordillera Oriental of the Ecuadorian Andes rises much like an irregular wall to the clouds and beyond to a series of volcanic peaks, some active and many perpetually covered with snow. West of this range is a complex system of intermontane valleys separating, and ridges connecting, the Cordillera Oriental and the Cordillera Occidental. In Ecuador the Cordillera Oriental is contiguous with the Colombian cordillera and continues southward with elevations above 3000 m from the Colombian border for about

275 km to the Pastaza trench. South of the Pastaza trench, elevations of more than 3000 m are continuous for another 150 km to the Río Paute Valley. From the Colombian border to the valley of the Río Paute are extensive areas of more than 4000 m and many snow-covered volcanoes exceeding 5000 m; these are (north to south) Volcán Cayambe (5789 m), Volcán Antisana (5705 m), Volcán Cotopaxi (5697 m), Cerro Altar (5319 m), and Volcán Sangay (5323 m). The latter, Volcán Reventador (3483 m), and Volcán Tunguragua (5005 m) have been active in the past decade. South of the Río Paute elevations above 3000 m are less extensive than to the north, and the highest peak is Cerro El Picacho (3850 m). One continuous range with elevations of more than 3000 m extends 130 km south-southwest from the Río Paute to the Río Zamora Valley, and another extends from that valley southward for about 125 km to the Huanca-bamba Depression in northern Perú. Three highland areas lie east of the main cordillera. Volcán Sumaco (3900 m) is situated on an eastern extension of the foothills and connected to the Cordillera

Oriental by elevations of more than 2000 m. The Cordillera Cutucú reaching elevations in excess of 1500 m is separated from the Cordillera Oriental by the valleys of the Río Upano and Río Naman-gosa at elevations of less than 1000 m. The Cordillera del Condor is separated from the Cordillera Oriental by the valleys of the Río Nangariza and Río Zamora at elevations of less than 1500 m.

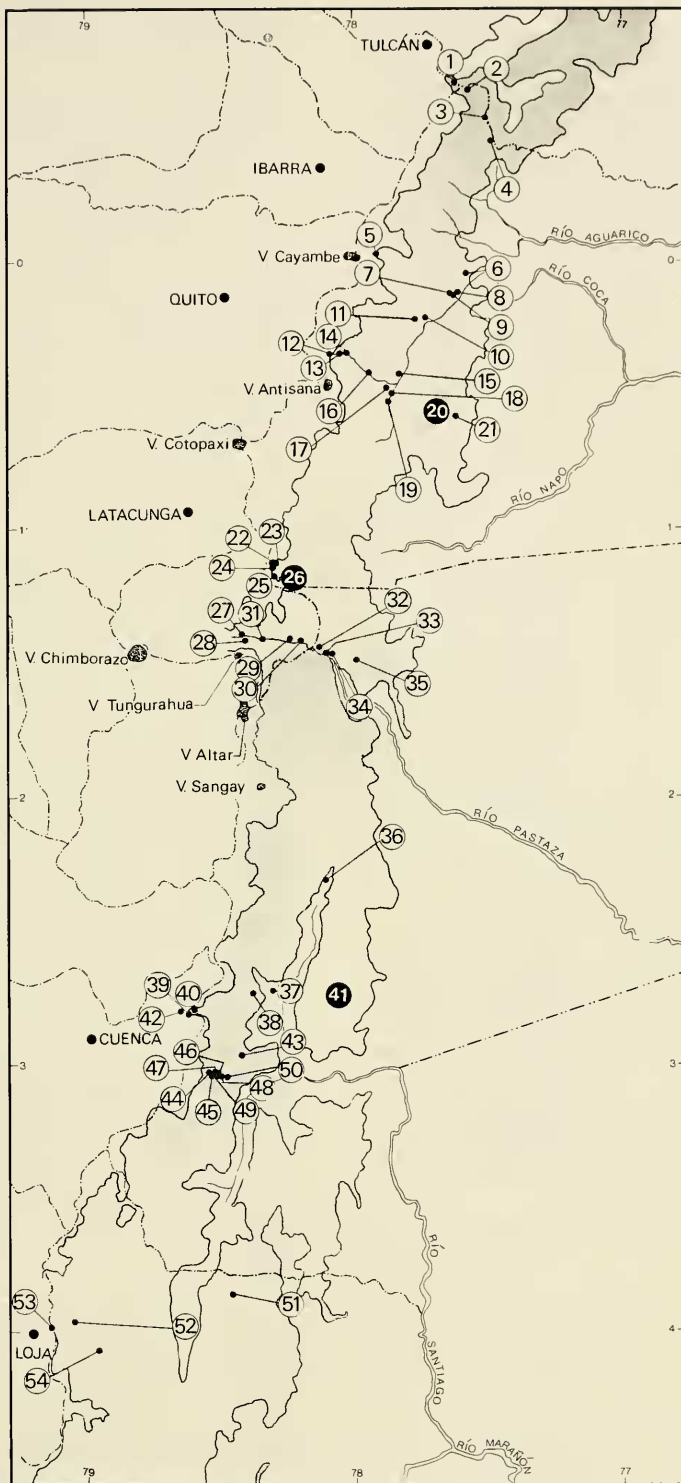
Countless small streams cascade down the eastern slopes of the Cordillera Oriental and coalesce to form small rivers, which in turn join to form larger rivers, all of which are tributaries of major rivers flowing into the Amazon—from north to south—Río Putumayo, Río Coca, Río Napo, Río Pastaza, Río Santiago, and Río Marañón. Three rivers have their head-waters in intermontane basins; the valleys of these rivers (Río Pastaza, Río Paute, Río Zamora) cut through the Cordillera Oriental thereby creating discontinuities in the high ranges. Of these, the Río Pastaza is the largest and most impressive, lying in a deep gorge between the Cerro Los Llanganati (4639 m) to the north and Volcán Tungurahua (5005 m) to the south. This valley, frequently referred to as the Pastaza trench, forms a lowland incision far into the Cordillera Oriental.

Only three climatological stations exist on the eastern slopes of the Andes in Ecuador; two of these (Baños and Pastaza) are in the Pastaza trench, and one (Papallacta) lies above 3000 m (Table 5). These data demonstrate the decline of temperatures (about 1°C for each 200 m) with increasing elevation

and show reduced rainfall but essentially equal relative humidity from lower to higher elevations. Baños, situated in the upper part of the deep Pastaza trench, certainly receives less rainfall than sites at the same elevation but situated on the montane slopes. In general the eastern slopes of the Andes from 1500 to 3000 m are bathed in clouds daily; usually mornings are relatively clear, but light rain may fall at any time of the day or night.

Between 1000 and 3000 m on the eastern slopes of the Andes the nature of the vegetation changes from tropical to subtropical. According to Holdridge's (1947, 1964) system of classification, the lower regions are humid subtropical forest and the upper reaches are very humid subtropical forest, as shown on an ecological map of Ecuador (Vivanco de la Torre et al., 1963). This is the altitudinal belt frequently referred to as cloud forest or montane rainforest. Below 1000 m the cloud forest gives way to tropical rainforest (humid tropical forest or very humid tropical forest in the classification of Holdridge). Above 3000 m the montane rainforest becomes dwarfed and at elevations of 3500–4000 m gives way to alpine formations, principally páramo. On the basis of the works of Acosta Solis (1968), Espinal and Montenegro (1963), Grubb and Whitmore (1966), and Grubb et al. (1963), the common genera of trees and shrubs at elevations below 2000 m include *Adenaria*, *Byrsönima*, *Calliandra*, *Cedrela*, *Guarea*, *Gynerium*, *Rapanea*, and *Salix*. Between 2000 and 3000 m the common genera

FIG. 6.—Map of the Amazonian slopes of the Andes in Ecuador. The area on the Amazonian slopes between 1,000 and 3,000 m is shaded. Numbers correspond to the following localities, arranged from northwest to southeast (see Gazetteer for details): 1. El Carmelo; 2. Santa Bárbara; 3. La Alegría; 4. La Bonita; 5. Agua Caliente; 6. Cordillera del Dué; 7. Río Reventador; 8. Río Azuela; 9. Salto de Agua; 10. Río Salado; 11. Santa Rosa; 12. Papallacta; 13. Chalpi; 14. Cuyujúa; 15. Borja; 16. Jatúntinahua; 17. Baeza; 18. Oritoyacu; 19. Río Bermejo; 20. Cerro Sumaco; 21. San José; 22. Río San José; 23. Paracayacu; 24. Río Jorge; 25. El Golpe; 26. Los Llanganatis; 27. Baños; 28. Runtun; 29. Río Negro; 30. El Topo; 31. Mirador; 32. Abitagua; 33. Mera; 34. Río Alpayacu; 35. Puyo; 36. Macas; 37. Méndez; 38. Mirador; 39. Cerro Negro; 40. Pailas; 41. Cordillera de Cutucú; 42. Sevilla de Oro; 43. General Plaza; 44. San Vicente; 45. Loma de Puerco; 46. Suro Rancho; 47. Sapote; 48. San Juan Bosco; 49. El Cruzado; 50. Plan de Milagro; 51. Río Piúntza; 52. Sabanilla; 53. Abra de Zamora; 54. Zamora.



are *Albizzia*, *Alchornia*, *Cupania*, *Inga*, *Miconia*, *Ochroma*, *Persea*, *Trema*, and *Trichanthera*. Tree ferns are abundant throughout the elevational range, whereas bromeliads are most abundant below 2000 m. Above 1800 m the viney bamboo, *Chusquea*, becomes more abundant, especially along streams, at high elevations. Physiognomically, the forest changes from lower to higher elevations (Grubb et al., 1963). In the lower montane rainforest (1000–±2000 m), the trees reach heights of 15–33 m and have small, if any, buttresses; leaves are notophyllic or mesophyllic, frequently have drip tips, and occasionally are compound. In the upper montane rainforest (2000–3000 m), the trees reach heights of 15–18 m and usually have no buttresses; leaves are microphyllic, few or none have drip tips, and few are compound. In the upper reaches of the forest (subalpine rainforest) the trees reach heights of 1.5–19 m and have no buttresses; leaves are nanophyllic, and none is compound or has a drip tip. Locally, due to winds and precipitation, a low (<1.5 m) subalpine type of elfin forest occurs on ridges above 2700 m; the low, gnarled bushes support heavy growths of mosses and large bromeliads.

Generally in the Neotropics many of the humid montane slopes are heavily cultivated in coffee, but on the Amazonian slopes of the Ecuadorian Andes, relatively little land is in *cafetales*; most of these are in the Pastaza trench, where cultivation is more extensive than elsewhere on the slopes. Other agricultural use of the land includes citrus planta-

tions, *naranjilla* (Solanaceae), dairy cattle, and subsistence farming.

PATTERNS OF DISTRIBUTION

To one unfamiliar with the diversity of *Eleutherodactylus* on the Andean slopes and with the topographic complexity of the region, the recognition of 45 species in a region about 500 km in length and 2000 m in elevation may be incomprehensible. Although *Eleutherodactylus* is the most speciose anuran genus in the region, *Colostethus* (Edwards, 1974) and *Centrolenella* (Lynch and Duellman, 1973) also are represented by many species there. Analysis of distributional data reveals that many species have rather restricted ranges latitudinally and/or altitudinally (Table 6). The major topographic barrier on the eastern face of the Andes in Ecuador is the Pastaza trench; thus, distributions were analyzed as: 1) north of the trench, 2) in the trench, and 3) south of the trench. Of the 31 species from north of the trench, 10 are endemic to the region and 10 are also known from Colombia; six of the latter are among 14 of the northern species also found in the Pastaza trench. Five of the 20 species in the trench are not found elsewhere on the Amazonian slopes of Ecuador, but three of these (*E. croceoinguinis*, *lacrimosus*, and *ockendeni*) are widely distributed at lower elevations; of the other two *E. trachyblepharis* occurs at elevations of 320–1300 m in the Pastaza Valley, whereas *E. pastazensis* is restricted to the upper part of the valley. Five

TABLE 5.—Summary of Climatic Date for Three Stations on Amazonian Slopes of Andes in Ecuador for 1971–1972.

(Data from INAMHI, 1973, 1975)

Station	Rainfall (mm)			Temperature (°C)	Atmospheric Humidity
	Mean An.	Driest	Wettest		
Papallacta 3160 m	1310	Dec. 64	Jul. 182	7.3–18.0 (\bar{x} = 9.1)	72–93 (\bar{x} = 88)
Baños 1843 m	1357	Nov. 46	Jul. 287	13.2–21.8 (\bar{x} = 16.8)	64–97 (\bar{x} = 86)
Pastaza 1043 m	4980	Sep. 140	Jun. 768	16.4–24.5 (\bar{x} = 20.0)	68–96 (\bar{x} = 86)

species in the trench are among the 15 species known from south of the trench, where eight species are endemic and three are shared with Perú. Only four species are found in and north and south of the trench (*E. galdi*, *nigrogriseus*, *quaquaversus*, and *w-nigrum*); the last species also occurs in Colombia.

Species that occur at lower elevations (<2000 m) tend to be more widespread than do those at higher elevations. Among the 13 species not ranging below 2000 m to the north of the trench, only two (*E. trepidotus* and *E. unistrigatus*) occur in the trench; those species are chiefly at higher elevations (>3000 m)

TABLE 6.—Distributional summary of 45 species of *Eleutherodactylus* on the eastern slopes of the Andes in Ecuador.
(* = also on Andean slopes in Colombia and ** = also in Perú)

Species	North of Pastaza Trench	In Pastaza Trench	South of Pastaza Trench
<i>E. acerus</i>	2660	-----	-----
<i>E. atratus</i>	-----	-----	2195-2850
<i>E. baryecucus</i>	-----	-----	2195-2990
<i>E. bromeliacus</i>	-----	-----	1710-2620
<i>E. chloronotus</i> *	2285-3000+	-----	-----
<i>E. colodactylus</i> **	-----	-----	2195-3000+
<i>E. condor</i>	-----	-----	1830
<i>E. cornutus</i> *	1150-1740	1100-1500	-----
<i>E. cremnobates</i>	1410-1700	-----	-----
<i>E. croceinguinis</i>	-----	-1000-1100	-----
<i>E. cryptomelas</i>	-----	-----	2470-3000+
<i>E. devillei</i>	2195-1980	-----	-----
<i>E. dolops</i> *	1100-1950	-----	-----
<i>E. elassodiscus</i> *	2300-2610	-----	-----
<i>E. eriphus</i>	2160-2600	-----	-----
<i>E. galdi</i>	1700-1740	1000-1280	1000-1830
<i>E. gladiator</i>	2360-2910	-----	-----
<i>E. glandulosus</i>	2105-2890	-----	-----
<i>E. ignicolor</i>	2160-2750	-----	-----
<i>E. incanus</i>	1700-1740	-----	-----
<i>E. incomptus</i> *	1410-1910	1270	-----
<i>E. inusitatus</i>	2160	1300	-----
<i>E. lacrimosus</i>	-----	-1000-1100	-----
<i>E. lanthanites</i> *	-1000-1490	-1000-1100	-----
<i>E. leoni</i>	2130-3000+	-----	-----
<i>E. leucopus</i> *	2400-2590	-----	-----
<i>E. lividus</i>	2135-2750	-----	-----
<i>E. nigrogriseus</i>	1150	1180-1800	2195-2835
<i>E. nigrovittatus</i>	-1000-1935	-1000-1100	-----
<i>E. ockendeni</i>	-----	-1000-1100	-----
<i>E. pastazensis</i>	-----	1800-1840	-----
<i>E. peruvianus</i> **	1410-1910	-----	1830
<i>E. petersi</i> *	1100-1935	1000-1800	-----
<i>E. prolatus</i>	1150-1490	1140	-----
<i>E. proserpens</i>	-----	-----	1700-2620
<i>E. pugnax</i>	1660-2540	-----	-----
<i>E. pycnodermis</i>	-----	-----	2650-3000+
<i>E. quaquaversus</i>	-1000-1740	-1000-1140	-1000-1830
<i>E. rubicundus</i>	1150	1000-1300	-----
<i>E. spinosus</i>	-----	-----	1700-2835
<i>E. trachyblepharis</i>	-----	-1000-1300	-----
<i>E. trepidotus</i>	2360-3000+	2925-3000+	-----
<i>E. unistrigatus</i> *	2710-3000+	1800-3000+	-----
<i>E. ventrimarmoratus</i> **	1740	-1000-1300	-1000-1100
<i>E. w-nigrum</i> *	1410-2540	1100-1600	2220

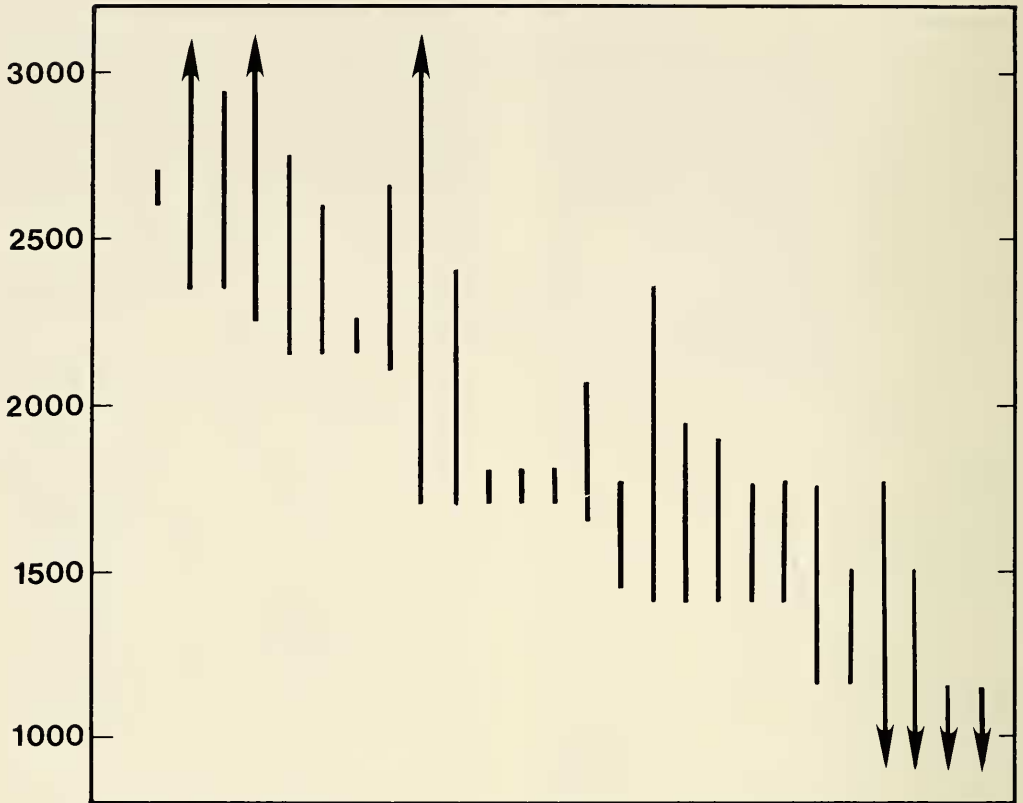


FIG. 7.—Altitudinal distribution of 26 species of *Eleutherodactylus* along a transect from Papallacta to the Cordillera del Dué. Each line represents one species. Arrows indicates that the range extends above 3000 m or below 1000 m.

and entered the trench from above. None of the six southern species occurring only above 2000 m is found in the trench.

Five species are primarily inhabitants of the upper Amazon Basin; *E. croceoinguinis*, *lacrimosus*, and *ockendeni* reach the slopes only in the Pastaza trench (elevations to 1100 m), whereas *E. lanthanites* occurs to elevations of 1490 m in Colombia and northern Ecuador, and to 1100 m in the Pastaza trench, and *E. ventrimarmoratus* ranges to 1300 m in the trench and to elevations of more than 1500 m in northern and southern Ecuador and in Perú.

It is evident that there are notable elevational changes in the *Eleutherodactylus* fauna on the eastern slopes of the Andes. In a transect in northern Ecuador, 26 species occur from 1000 to 3000 m (Fig. 7); a transect in southern Ecu-

dor contains 11 species; in the former transect no more than 14 species have been found at any given elevation (1700–1800 m), whereas in the latter transect six species occur at 2200–2300 m. A more realistic analysis compares the fauna at specific sites along the northern transect (Table 7; Fig. 8). The maximum number of species at any given site is 11 at the Río Azuela, 1740 m; four other sites have seven species, and one has six species.

ELEUTHERODACTYLINE COMMUNITIES

Several eleutherodactyline communities are apparent on the Amazonian slopes to the Andes. There are listed below.

1. Upper cloud forest, Provincia Mo-

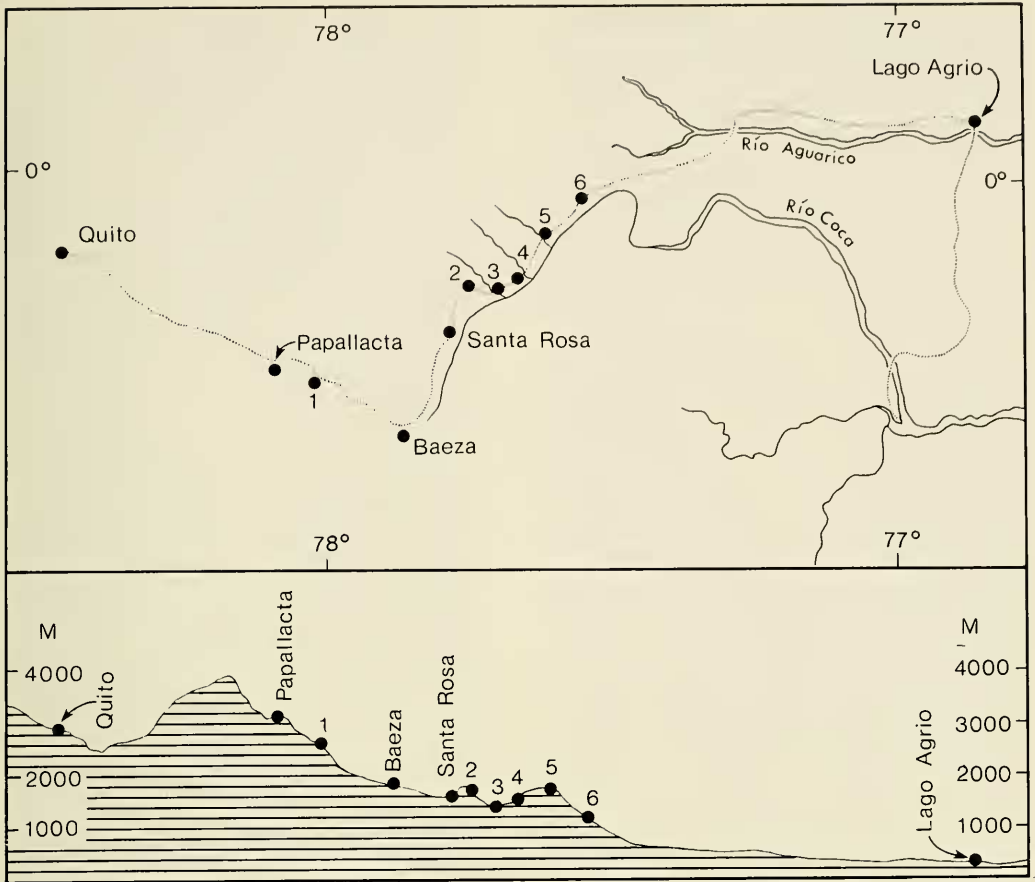


FIG. 8.—Map and profile of transect from Quito to Lago Agrio showing sites compared in Table 5. 1. 11–12 km ESE Papallacta, 2660 m. 2. 16.5 km NE Santa Rosa, 1700 m. 3. Río Salado, 1410 m. 4. 2 km WSW Río Reventador, 1490 m. 5. Río Azuela, 1740 m. 6. Cordillera del Dué, 1150 m.

rona-Santiago (2000–3000 m): *E. atratus*, *E. baryecus*, *E. bromeliaceus*, *E. colodactylus*, *E. cryptomelas*, *E. nigrogriseus*, *E. proserpens*, *E. pycnodermis*, *E. spinosus*, and *E. w-nigrum*.

2. Upper cloud forest, Provincia Napo north to Nevado Cayambe (2000–3000 m): *E. acerus*, *E. chloronotus*, *E. devillei*, *E. elassodiscus*, *E. eriphus*, *E. gladiator*, *E. glandulosus*, *E. ignicolor*, *E. lividus*, *E. pugnax*, *E. trepidotus*, and *E. w-nigrum*.

3. Upper cloud forest, northern Provincia Napo and southern Colombia (2000–3000 m): *E. buckleyi*, *E. chloronotus*, *E. elassodiscus*, *E. leoni*, *E. leucopus*, *E. pugnax*, *E. unistrigatus*, *E. sp. (vertebralis-like)*, and *E. w-nigrum*.

4. Lower cloud forest, Pastaza valley north into Colombia (1300–2000 m): *E. cornutus*, *E. cremnobates*, *E. dolops*, *E. galdi*, *E. incanus*, *E. incomptus*, *E. inusitatus*, *E. nigrogriseus*, *E. pastazensis*, *E. peruvianus*, *E. petersi*, *E. prolatus*, *E. quaquaversus*, and *E. w-nigrum*.

5. Lowest cloud forest (1000–1300 m): *E. rubicundus*, *E. trachyblepharis*, and *E. ventrimarmoratus*. These are joined by some predominately lowland rainforest species at some localities—*E. croceinguinis*, *E. lacrimosus*, *E. lanthanites*, *E. nigrovittatus*, and *E. ockendeni*.

Eleutherodactylus w-nigrum is common to four (1–4) of the communities. Communities 2 and 3 share *E. chloronotus*, *E. elassodiscus*, and *E. pugnax* in ad-

dition to *E. w-nigrum*; they remain amply distinct—only part of the distinction is explicable in terms of β -diversity (species turnover between localities). It seems most unlikely that several of the species have been missed by collectors, although that may well be the case for such species as *E. eriphus* and *E. ignicolor*.

Except for *E. pycnodermis*, all species of community 1 were collected at Sapote (locality 47). All but *E. cryptomelas* and *E. pycnodermis* were found at El Cruzado (locality 49). *Eleutherodactylus pycnodermis* was found at nearby Suro Ranch (locality 46) with four other members of the community. All but *E. pugnax* of community 2 have been collected in the immediate vicinity of Cuyujúa, Prov. Napo (locality 14). The species of community 3 have been collected from several localities between El Carmelo and Santa Barbara, but no site has yielded all. No locality has produced all the species for community 4; nine of the species were found at the Río Azuela. *Eleutherodactylus inusitatus* and *E. pastazensis* are both rare (three and four specimens respectively); *E. nigrogriseus* is common to the south but quite rare north of the Pastaza trench. Community 5 may not be distinct from community 4 but does include five lowland species that extend up into the cloud forest (six if *E. ventrimarmoratus* is considered a lowland species). The overlap of communities 4 and 5 is especially evident in the eleutherodactyline fauna found at Mera, Provincia Pastaza (locality 33): *E. croceinguinis*, *E. lacrimosus*, *E. lanthanites*, *E. nigrovittatus*,

E. ockendeni, *E. peruvianus* (old specimens, UMMZ), *E. petersi*, *E. prolatus*, *E. quaquaversus*, *E. rubicundus*, *E. trachyblepharis*, and *E. ventrimarmoratus* (four species of community 4 and eight of community 5).

Habitat partitioning by these species essentially occurs along spatial and trophic dimensions, because with the exception of *E. nigrovittatus* all appear to be nocturnal. During the daylight hours all others are found in sites of concealment (beneath rocks and logs or in axillae of plants).

Spatial (microhabitat) separation is not pronounced. In community 2, *E. elassodiscus* and *E. trepidotus* are terrestrial, *E. pugnax* and *w-nigrum* are very closely associated with streams, and the remaining eight species are found on low vegetation (not necessarily close to streams). In community 3, *E. elassodiscus*, *E. pugnax*, and *E. w-nigrum* behave as in community 2, and the remaining six species are found on low vegetation.

In community 4, *E. cornutus* and *E. dolops* are terrestrial, *E. cremnobates*, *E. nigrogriseus*, and *E. w-nigrum* are closely associated with streams (on vegetation), and the other nine species are active on vegetation (presumably *E. pastazensis* is active on vegetation at night—no data are available).

In community 5, *E. nigrovittatus* is terrestrial and diurnal, *E. rubicundus* usually is found on vegetation above or beside streams and seeps, and the remaining six species are found on low vegetation.

TABLE 7.—Comparison of the numbers of species of *Eleutherodactylus* at six sites along a transect from Papallacta to the Cordillera del Dué, Ecuador.¹

	1.	2.	3.	4.	5.	6.
1. (11-12 km ESE Papallacta, 2660 m)	7	<i>.00</i>	<i>.00</i>	<i>.00</i>	<i>.00</i>	<i>.00</i>
2. (Río Azuela, 1740 m)	0	11	<i>.67</i>	<i>.44</i>	<i>.55</i>	<i>.23</i>
3. (16.5 km NE Santa Rosa, 1700 m)	0	6	7	<i>.43</i>	<i>.85</i>	<i>.15</i>
4. (2 km WSW Río Reventador, 1490 m)	0	4	3	7	<i>.57</i>	<i>.31</i>
5. (Río Salado, 1410 m)	0	5	6	4	7	<i>.15</i>
6. (Cordillera del Dué, 1150 m)	0	2	1	2	1	6

¹ Boldface numbers are actual numbers of species at a site; Roman numbers are the number of species in common between sites, and italicized numbers are the coefficients of community (Whittaker, 1970).

No direct data on trophic separation are available. Duellman (1978) found little trophic separation at Santa Cecilia but such a finding might have been predicted because his food classes were not precise. Indirect data are available in the form of size differences between species. Lynch (1976d, 1979a) compared communities and ecological contingencies on the basis of ϕ values (ϕ = mean size of larger/mean size of smaller; see Hutchinson and MacArthur, 1959, for theory). The frogs in these five communities exhibit comparable size differences in each community (Table 8). Mean ϕ values range from 1.08 to 1.15. Separating members of the communities by both size and microhabitat elevates mean ϕ values principally because the species associated with streams as well as the terrestrial taxa exhibit more pronounced size differences among themselves than do the species found on vegetation (contingency 3, Table 8).

Frogs of the *unistrigatus* group are predominant in each of the five communities (Table 9) but few close relatives are sympatric. Only four assemblies in the five communities have more than one species per community (*diadematus*, *glandulosus*, *nigrogriseus*, and *trachyblepharis* assemblies). The sympatric members of the *diadematus* assembly (community 5) are *E. croceinguinis* and *E. ventrimarmoratus*; they differ markedly

in size (Table 3). As many as five species of this assembly (*E. altamazonicus*, *E. croceinguinis*, *E. diadematus*, *E. martiae*, and *E. ventrimarmoratus*) may co-occur in the vicinity of Puyo, Provincia Pastaza (900 m); the size differences between adjacent-sized species is greater (Table 10) than those for entire community assemblages on the Amazon slopes (Table 8) or in the lowlands (Lynch, 1979a).

Three species of the *glandulosus* assembly are sympatric in community 3 (*E. acerus*, *E. glandulosus*, and *E. lividus*). These frogs are moderately well-separated by size (*acerus-glandulosus*, ϕ 1.14 male, 1.25 female; *glandulosus-lividus*, ϕ 1.38 male, 1.06 female), but only *E. glandulosus* is sufficiently abundant for us to have confidence in its body size. Two species of the *nigrogriseus* assembly (*E. nigrogriseus* and *E. spinosus*) are sympatric in community 1; they are nearly equal in size ($\bar{x} \phi$ = 1.11). Two species of the *celator* assembly are also sympatric in community 1; their size difference is likewise slight ($\bar{x} \phi$ = 1.08). The two species of the *trachyblepharis* assembly sympatric in community 4, *E. galdi* and *E. prolatus*, differ markedly in size ($\bar{x} \phi$ = 1.34).

Our current knowledge of these frogs leaves the impression of only slight habitat partitioning in communities in the cloud forests and lowland forests. Parti-

TABLE 8.— ϕ values for Amazonian Slope Eleutherodactyline Communities. Values include range (N) mean.

	Contingency		
	1. Size alone; all species	2. Size and microhabitat; all species	3. Size and microhabitat; orboreal species only
Community 1 ♂♂	1.01-1.26(9)1.09	-----	-----
Community 2 ♂♂	1.00-1.18(10)1.08	1.00-1.59(9)1.19	1.00-1.25(7)1.10
Community 3 ♂♂	1.00-1.33(8)1.10	1.06-1.37(6)1.19	1.06-1.33(5)1.15
Community 4 ♂♂	1.00-1.34(11)1.08	1.00-1.51(10)1.12	1.00-1.51(7)1.10
Community 5 ♂♂	1.01-1.33(8)1.12	1.01-1.33(7)1.14	1.01-1.33(7)1.14
Community 1 ♀♀	1.02-1.45(9)1.13	-----	-----
Community 2 ♀♀	1.00-1.24(10)1.09	1.00-1.58(8)1.21	1.00-1.24(6)1.10
Community 3 ♀♀	1.00-1.22(8)1.11	1.00-1.56(6)1.23	1.00-1.36(5)1.16
Community 4 ♀♀	1.00-1.33(12)1.08	1.00-1.58(10)1.14	1.00-1.33(8)1.09
Community 5 ♀♀	1.00-1.36(8)1.15	1.00-1.36(7)1.17	1.00-1.36(7)1.17

tioning seems to be more complete in páramo communities comprised of few species (Duellman, 1979). The large number of species of *Eleutherodactylus*, as well as many other kinds of frogs, in cloud forests (and in lowland rainforest in the upper Amazon Basin) may have both historical and ecological explanations. According to the refugia theory (Haffer, 1969, 1974), the lower Amazonian slopes and adjacent Amazon Basin in Ecuador supported tropical rainforest throughout the Pleistocene, whereas forests in much of the Amazonian region diminished during arid phases of the Pleistocene. Lynch (1979b) showed a high fidelity of *Eleutherodactylus* to humid forests and high degrees of endemism to area of proposed refugia. Our

limited data on habitat partitioning among *Eleutherodactylus* parallels that presented for a lowland Amazon site by Duellman (1978), who interpreted the low ϕ values and broad niche overlap values in a large anuran community as being indicative of bountiful resources and little interspecific competition. Although we have no precise measurements of the structural heterogeneity of the forests on the Amazonian slopes of the Andes, we are impressed with the general trend from greater heterogeneity at lower elevations (<1800 m) to less heterogeneity at higher elevations (> 1800 m) and diminution of the forest above 3000 m. In general there is a decline in the numbers of species of *Eleutherodactylus* from low to high elevations. It has yet to be demonstrated whether frogs are responding directly to heterogeneity of the habitat or both frogs and vegetation are responding to physical environmental factors.

TABLE 9.—Distribution of species groups and assemblies in five Amazonian slope eleutherodactyline communities.

	Community				
	1	2	3	4	5
<i>biporcatus</i> group	0	0	0	1	0
<i>discoidalis</i> group	0	1	1	1	1
<i>fitzingeri</i> group	1	1	1	2	1
<i>unistrigatus</i> group	9	10	7	10	6
<i>acuminatus</i> assembly	1	---	---	1	---
<i>celator</i> assembly	2	---	---	---	---
<i>crucifer</i> assembly	1	1	1	1	---
<i>curtipes</i> assembly	---	1	1	---	---
<i>devillei</i> assembly	---	1	1	---	---
<i>diadematus</i> assembly	---	---	---	1	2
<i>frater</i> assembly	---	---	---	1	1
<i>glandulosus</i> assembly	---	3	1	---	---
<i>lacrimosus</i> assembly	1	---	---	1	1
<i>nigrogriseus</i> assembly	2	1	---	1	---
<i>pugnax</i> assembly	---	1	1	---	---
<i>pyrrhomerus</i> assembly	---	1	1	---	---
<i>rubicundus</i> assembly	---	---	---	1	1
<i>surdus</i> assembly	1	---	---	---	---
<i>trachyblepharis</i> assembly	---	1	---	2	1
<i>unistrigatus</i> assembly	1	---	1	1	---

RESUMEN

El género *Eleutherodactylus* está representado en las laderas amazónicas de los Andes Ecuatorianos por no menos de 47 especies. En este informe damos registros de 45 de las 47 especies, incluyendo las descripciones de 12 especies nuevas (*E. acerus*, *E. condor*, *E. cremnobates*, *E. dolops*, *E. eriphus*, *E. ignicolor*, *E. incanus*, *E. incomptus*, *E. inusitatus*, *E. lividus*, *E. petersi*, *E. prolatus*), y descripciones igualmente detalladas de cuatro especies poco conocidas (*E. pastazensis*, *E. peruvianus*, *E. rubicundus*, *E. trachyblepharis*). Las especies nuevas incluyen un miembro del grupo *discoidalis* (*E. dolops*), un miembro del grupo

TABLE 10.—Size differences among sympatric members of the *diadematus* assembly. Overall $\bar{x} \phi$ (8 comparisons) = 1.16.

	$\bar{x} \text{ } \phi$ SVL	$\phi \text{ } \phi$	$\bar{x} \text{ } \delta$ SVL	$\phi \text{ } \delta$	$\bar{x} \text{ } \phi$
<i>E. diadematus</i>	39.8	1.08	23.5	1.08	1.08
<i>E. ventrimarmoratus</i>	36.9	1.32	21.8	1.16	1.24
<i>E. altamazonicus</i>	27.9	1.37	18.8	1.24	1.30
<i>E. martiae</i>	20.4	1.03	15.1	1.03	1.03
<i>E. croceoinguinis</i>	19.8	---	14.6	---	---

fitzingeri (*E. condor*), y 10 miembros del grupo *unistrigatus*. Sinónimas, diagnósticos, coloración en vida, distribuciones, y notas ecológicas, así como referencias a descripciones previamente publicadas son dadas para *E. chloronotus*, *E. cornutus*, *E. croceinguinis*, *E. devillei*, *E. elassodiscus*, *E. galdi*, *E. gladiator*, *E. glandulosus*, *E. lacrimosus*, *E. lanthanites*, *E. leoni*, *E. leucopus*, *E. nigrogriseus*, *E. nigrovittatus*, *E. pugnax*, *E. quaquaversus*, *E. trepidotus*, *E. unistrigatus*, *E. ventrimarmoratus*, and *E. w-nigrum*. Las poblaciones de *E. lacrimosus*, *E. lanthanites*, *E. nigrovittatus*, and *E. peruvianus* de las laderas amazónicas son de mayor tamaño a aquellas poblaciones de las tierras bajas.

Las 47 especies incluyen representantes de cuatro grupos de especies (los grupos *biporcatus*, *discoidalis*, *fitzingeri*, y *unistrigatus*). El grupo *unistrigatus* está representado por 16 subgrupos; 71 especies del grupo *unistrigatus* pertenecen a estos 16 subgrupos—44 son animales de bosque nublado, 12 son especies de páramo y subpáramo, y 15 especies son de la selva de tierras bajas.

El Valley del Río Pastaza es la barrera más importante de las laderas amazónicas, y su efecto es más notorio en las especies que se encuentran en alturas medias (2000–3000 m). Cinco unidades ecogeográficas son aparentes y están parcialmente correlacionadas con tres estratas altitudinales y de vegetación. Las comunidades de ranas eleutherodactylinas en cada una de las unidades ecogeográficas son distintas entre sí. Las

cinco comunidades que reconocemos son: 1) bosque nublado superior, Provincia Morono-Santiago, 2000–3000 m, 10 especies; 2) bosque nublado superior, Provincia Napo, hacia el norte hasta el Nevado Cayambe, 2000–3000 m, 12 especies; 3) bosque nublado superior al norte de la Provincia Napo y de Colombia adyacente, 2000–3000 m, 8 especies; 4) bosque nublado inferior al norte del Río Pastaza, 1300–2000 m, 14 especies; y 5) bosque nublado bajo, 1000–1300 m, 8 especies.

Entre estas comunidades hay una ligera separación ecológica, excepto una, son nocturnas. Solamente una o dos especies terrestres (o una o dos especies estrechamente relacionadas con arroyos) por comunidad son separadas por microhabitat. Gran parte de los miembros de cada comunidad son ranas arborícolas las cuales se encuentran en vegetaciones bajas. Diferencias en tamaño (reflejadas por diferencias del tamaño de la preza) son muy sutiles (especies de tamaños similares en las cuales la mayor es aproximadamente 130 por ciento del tamaño de la menor, promedio = 110%). Si consideramos simultáneamente el tamaño y el microhabitat hay una ligera separación la cual es aparente (110–120%).

El número de especies generalmente disminuye a medida que aumenta la elevación. Hay disminución en la heterogeneidad estructural del bosque. Las ranas responden a esa heterogeneidad o ambos pueden estar respondiendo a gradientes en los factores físicos del medio.

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APPENDIX A: SPECIMENS EXAMINED

Eleutherodactylus acerus (4 spec.)

ECUADOR, *Prov. Napo*: 7.8 km WNW Cuyujúa, 2750 m, KU 143517; 11 km ESE Papallacta, 2660 m, KU 165471-73.

Eleutherodactylus atratus (44 spec.)

ECUADOR, *Prov. Morona-Santiago*: El Cruzado, 2195 m, USNM 199690-99; San Vicente, 2835 m, USNM 199712; Sapote, 2470 m, USNM 199701-10, 199713 (cleared and stained skeleton); 2 km W Sapote, 2561 m, USNM 199711; between Sapote and Suro Rancho, 2604-2622 m, USNM 199683-89; Suro Rancho, 2683 m, USNM 199675-82; 0.5 km W Suro Rancho, 2744 m, USNM 199700; *Prov. Zamora-Chinchiipe*: Abra de Zamora, 2850 m, KU 165236-38, 166265 (cleared and stained skeleton).

Eleutherodactylus baryecus (17 spec.)

ECUADOR, *Prov. Morona-Santiago*: Cerro

Negro, 2927 m, USNM 199715; El Cruzado, 2195 m, USNM 199723-24; San Juan Bosco, 2195 m, USNM 199725; between San Juan Bosco and El Cruzado, 2226 m, USNM 199717-22; San Vicente, 2805-2835 m, USNM 199729; 3 km W San Vicente, 2988 m, USNM 199730; Sapote, 2470 m, USNM 199726-28; between Sevilla de Oro and Mendez (probably between the crest and Pailas), USNM 199716; Suro Rancho, 2683 m, USNM 199714.

Eleutherodactylus bromeliaceus
(23 spec.)

ECUADOR, *Prov. Morona-Santiago*: El Cruzado, 2195 m, USNM 199738-39; Mirador, 1982 m, USNM 199735; Pailas, 2195 m, USNM 199732-34, 199743-45; Plan de Milagro, 1707 m, USNM 199736-37, 199746-47; Río Piúntza, Cordillera del Condor, 1830 m, KU 146974-75; 0.5 km E Sapote, 2393 m, USNM 199740, 199748-49; 1 km E Sapote, 2332 m, USNM 199741; mountain above Sapote (to the south),

2500 m, USNM 199742, 199750; between Sapote and Suro Rancho, 2622 m, USNM 199731; *Prov. Zamora-Chinchipe*: 22 km W Zamora, 1730 m, KU 141772.

Eleutherodactylus chloronotus
(231 spec.)

COLOMBIA, *Depto. Nariño*: 12 km E Pasto, 3050 m, KU 167972-8002, 170127-29 (cleared and stained skeletons); *Depto. Putumayo*: 13 km W Santiago, 2900 m, KU 165003-08.

ECUADOR, *Prov. Napo*: 2 km E Chalpi, 2700 m, USNM JAP 5547-48, 5550; 4 km E Chalpi, 2590 m, USNM JAP 5553, 5558; Chaspi Chico bridge, 4.6 km E Papallacta, 2870 m, MCZ 92117; Cuyujúa, UIMNH 55823-24, 55846; 1 km E Cuyujúa, 2285 m, USNM JAP 5531; 7.8 km WNW Cuyujúa, 2750 m, KU 143317-25; Laguna del San Marcos, NE of Cayambe, CAS-SU 8287; Llanganati mountains, El Golpe, 3000 m, CAS-SU 17433; Llanganati mountains, Río Jorge, 3000 m, CAS-SU 17444; Llanganati mountains, at Río San Jose, 3049 m, CAS-SU 10385-89, 10391, 10401-08, 17395-425, 17444; Papallacta, 3110-3130 m, KU 143331-49, USNM JAP 5108, 5110, 5113-14; 0.5 km E Papallacta, 3095 m, USNM JAP 5128; 1.6 km E Papallacta, 2980 m, KU 177242-44; 3 km E Papallacta, 2900 m, KU 117516-49, 118103(5), 118104-06 (lots of eggs), 118130-33 (cleared and stained skeletons); 5.7 km E Papallacta, 2910 m, KU 143326-30; 9.2 km ESE Papallacta, 2750 m, KU 177246; 9.6 km E[SE] Papallacta, 2700 m, MCZ 92116; 11 km ESE Papallacta, 2660 m, KU 155436-40, 165208-18, 166267-68 (cleared and stained skeletons), 177245; 12 km ESE Papallacta, 2630 m, KU 165202-07; 15 km E[SE] Papallacta, 2600 m, KU 127007-11; 1 km W Papallacta, 3200 m, KU 111385-86; 2 km W Papallacta, 3270 m, KU 177247; 4 km W Papallacta, 3300 m, KU 117550-56; north side Laguna Papallacta, 3350 m, KU 109071-72; Río Bermejo, Cordillera Guacamayo, WCAB 35651; 0.8 km NW Santa Barbara, Quebrada El Corazon, 2540 m, KU 177248.

Eleutherodactylus colodactylus
(113 spec.)

ECUADOR, *Azuay Prov.*: 8 km ESE Sevilla de Oro (on Azuay, Morona-Santiago frontier), 3140 m, USNM 198458. *Morona-Santiago Prov.*: El Cruzado, 2195 m, USNM 198436; Pailas, 2195 m, USNM 198431-33, 198459; San Juan Bosco, 2195 m, USNM 198434-35, 198460-61; immediate environments of San Vicente, 2790-2820 m, USNM 198465-79; 1 km W San Vicente, 2851 m, USNM 198462-64; 1 km E Sapote, 2332 m, USNM 198457; mountain above Sapote to the south, 2500 m, USNM 198456; 1/2 km W Sapote, 2546 m, USNM

198437-55. *Zamora-Chinchipe Prov.*: Abra de Zamora, 2800 m, KU 142151-59 (142155 is cleared and stained skeleton), 165219-21; 14 km E Loja, 2770 m, KU 142160-61; 15 km E Loja, 2710 m, KU 142162-64.

PERÚ, *Depto. Piurá*: 33 km SW Huanca-bamba, 2745-3050 m, LSUMZ 32368-414.

Eleutherodactylus condor (46 spec.)

ECUADOR, *Prov. Morona-Santiago*: Pastaza River, Canelos to Marañon, MCZ 19629-30, 19632; Río Piuntza, Cordillera del Condor, 1830 m, KU 146991-7033.

Eleutherodactylus cornutus (46 spec.)

COLOMBIA, *Depto. Putumayo*: 10.3 km W El Pepino, 1440 m, KU 168009.

ECUADOR, no specific locality: USNM 167431; *Prov. Morona-Santiago*: Cutucú mountains, E of Macas, 1800-2000 m, AMNH 39499; Macuma, USNM 167401-08; Miazal, USNM 167409-27; *Prov. Napo*: Cerro Sumaco, AMNH 22265-70; S slope Cerro Sumaco, USNM 167429; S slope Cordillera del Dué above Río Coca, 1150 m, KU 123447-48; Loreto, USNM 167428; Río Azuela, 1740 m, KU 143350; 2 km SSW Río Reventador, 1490 m, KU 165222; *Prov. Pastaza*: Canelos, USNM 167430; 10 km S Veracruz, MCZ 89972; *Prov. Tungurahua*: El Topo, 1270 m, BM 1912.11.1.57; Mirador, Baños, 1500 m, BM 94.10.30.44.

Eleutherodactylus cremnobates
(40 spec.)

ECUADOR, *Prov. Napo*: 7 km SW Río Azuela, KU 155456-60; 2 km SSW Río Reventador, 1490 m, KU 166036-56; Río Salado \pm 1 km upstream from Río Coca, 1410 m, KU 146164, 177249-60; 16.5 km NNE Santa Rosa, 1700 m, KU 143459.

Eleutherodactylus croceinguinis
(66 spec.)

Only Amazonian slope specimens are listed here; see Lynch (1980) for lowland localities. 200 lowland specimens also examined.

ECUADOR, *Prov. Pastaza*: Mera, 1140 m, KU 119527-30, 119534-43, 119546-72, 121352 (eggs), 121353 (juveniles), 177261-74; 1 km W Puyo, 1000 m, MCZ 90008-11; 25 km NNE Puyo, 1040 m, KU 146093; Río Alpayacu, 1 km E Mera, 1100 m, KU 119531-33.

Eleutherodactylus cryptomelas (9 spec.)

ECUADOR, *Prov. Morona-Santiago*: Sapote, 2470 m, USNM 198480-82; 2 km W Sapote, 2560 m, USNM 198483; *Prov. Loja*: 7 km N San Lucas, 2840 m, KU 177735; 8-9 km M San Lucas, 3000-3100 m, KU 120095-96; *Prov.*

Zamora-Chinchipec: Abra de Zamora, 2710 m, KU 141992-93.

Eleutherodactylus devillei (146 spec.)

ECUADOR, "Andes of Ecuador": MRHN 1009; *Prov. Napo*: Baeza, WCAB 35531; Borja, 1710 m, USNM JAP 5670; 2 km E Chalpi, 2700 m, USNM JAP 5535, 5546, 5549; 4 km E Chalpi, 2620 m, USNM JAP 5156-59, 5552, 5556-57, 5559, 5565-74, 5576-83; Chaspi Chico bridge, 4.6 km E Papallacta, 2870 m, KU 143408-14, MCZ 92118-23; Cuyujúa, 2360 m, UIMNH 55825-35 (55833, cleared and stained skeleton), USNM JAP 5209, 5295, 5298, 5314, 5316, 5607, 5615, 5699-5700, 5762-64; 0.4 km ESE Cuyujúa, 2460 m, KU 178999; 1 km E Cuyujúa, Río Victoria, 2420 m, KU 146095; 1.5 km E[SE] Cuyujúa, 2440 m, USNM JAP 5262-73; 3 km E[SE] Cuyujúa, 2285 m, USNM JAP 5257; 3.3 km ESE Cuyujúa, 2350 m, KU 143393; 7 km E[SE] Cuyujúa, 2195 m, USNM JAP 5358; 1 km W Cuyujúa, 2500 m, USNM JAP 5303-05; 2.5 km WNW Cuyujúa, 2550 m, KU 143394-99; 5 km W[NW] Cuyujúa, 2745 m, USNM JAP 5746-52; 7.8 km WNW Cuyujúa, 2750 m, KU 143400; "top" of Mt. Sumaco, AMNH 22192; 1.6 km E Papallacta, 2980 m, KU 177275; 3 km E[SE] Papallacta, 2900 m, KU 117570-71; 5.7 km ESE Papallacta, 2910 m, KU 143401-07; 8.3 km ESE Papallacta, Río Chalpi, 2750 m, KU 177276-77; 9.2 km ESE Papallacta, 2750 m, KU 177278; 9.6 km ESE Papallacta, 2700 m, MCZ 92124; 11 km ESE Papallacta, 2660 m, KU 165408-14, 165933-34, 166271-72 (cleared and stained skeletons), JDL 9422; 12 km ESE Papallacta, 2630 m, KU 155441, 166269-70 (cleared and stained skeletons); 13.1 km ESE Papallacta, 2610 m, KU 177279-80; 15 km E[SE] Papallacta, 2600 m, KU 127012-13; 1 km W Papallacta, 3155 m, USNM JAP 5150-51; Río Bermejo, Cordillera Guacamayo, WCAB 35653; Santa Barbara, 2590 m, USNM JAP 4478.

Eleutherodactylus dolops (11 spec.)

COLOMBIA, *Depto. Putumayo*: 10.3 km W El Pepino, 1440 m, KU 168811; 35 km SE San Francisco, 1950 m, KU 168809-10.

ECUADOR, *Prov. Napo*: Loreto, USNM GOV 8901; Río Azuela, 1740 m, KU 143504; 2 km SSW Río Reventador, 1490 m, KU 165866-68; Salto de Agua, 2.5 km NNE Río Reventador, 1660 m, KU 143505; *Prov. Pastaza*: Río Villano, USNM GOV 9332-33.

Eleutherodactylus ellassodiscus
(44 spec., only 17 extant)

COLOMBIA, *Depto. Putumayo*: 13 km W Santiago, 2900 m, KU 168012-13.

ECUADOR, *Prov. Napo*: Borja, 1720 m, JAP 5671-72; Cuyujúa, 2380 m, JAP 5206,

5210-13, 5228, 5294, 5299-300, 5315, 5472-74, 5701-02, KU 130271-72, USNM 167668-69; 0.4 km ESE Cuyujúa, 2460 m, KU 177282-85; 1 km E[SE] Cuyujúa, 2300 m, JAP 5236, 5238-42, USNM 167670 (cleared and stained skeleton); 3 km E[SE] Cuyujúa, 2300 m, JAP 5252-55; 3.3 km ESE Cuyujúa, 2350 m, KU 143415, 146097; Papallacta, WCAB 37915; Santa Barbara, 2610 m, USNM 192907-08; 1 km NW Santa Barbara, 2610 m, USNM 192906. [All specimens identified as JAP were lost in the mails in 1970 (Lynch, 1973a)].

Eleutherodactylus eriphus (15 spec.)

ECUADOR, *Prov. Napo*: Papallacta, WCAB 37903, 37905, 37907-09; 12 km E[SE] Papallacta, KU 155451-55; Río Jatuntinahua, 10 km ESE Cuyujúa, 2160 m, KU 166031-35.

Eleutherodactylus galdi (39 spec.)

ECUADOR, no other locality: AMNH 17444; *Prov. Morona-Santiago*: El Cruzado, 2195 m, USNM JAP 7276; Miazal, USNM GOV 8947; Pailas, 2195 m, USNM JAP 6567-69, 6621-22; Río Piüntza, Cordillera del Condor, 1830 m, KU 146977-85; San José de Cuchipamba, MSNT 513(3776); *Prov. Napo*: Loreto, CAS-SU 13155, USNM GOV 8945-46, 8944 (cleared and stained skeleton), JAP 3893, 8828, WCAB 39910; Mt. Sumaco, side of, AMNH 22334; Mt. Sumaco, S slope, 800-1000 m, CAS-SU 13154; "top" of Mt. Sumaco, AMNH 22201, 22205-08; Río Azuela, 1740 m, AMNH 89726, KU 143416, 165422; *Prov. Pastaza*: Río Upano, Macas, 1000 m, AMNH 21496; *Prov. Tungurahua*: El Topo, 1280 m, BM 1912.11.1.54-55 (reregistered as 1947.2.16.78-79); *Prov. Zamora-Chinchipec*: Sabanilla, AMNH 13531.

Eleutherodactylus gladiator (6 spec.)

ECUADOR, *Prov. Napo*: 5 km E[SE] Chalpi, 2560 m, USNM JAP 5256; Cuyujúa, 2360 m, USNM JAP 5608; 3.3 km ESE Cuyujúa, 2350 m, KU 143516; 5.7 km ESE Papallacta, 2910 m, KU 143513-15.

Eleutherodactylus glandulosus
(187 spec.)

ECUADOR, "Andes of Ecuador": MRHN 1010; *Prov. Napo*: Borja, 1710 m, USNM JAP 5673-83; 2 km E Chalpi, 2700 m, USNM JAP 5289-90; 4 km E Chalpi, 2620 m, USNM JAP 5560; Cuyujúa, 2360 m, UIMNH 55836-45, 55847-49, USNM JAP 5301-02, 5589-93, 5595-603, 5616-20, 5684-97, 5766-69; 0.4 km ESE Cuyujúa, 2460 m, KU 177291-95; 1 km E[SE] Cuyujúa, 2285 m, USNM JAP 5233-35, 5321-30; 3 km E[SE] Cuyujúa, 2285 m, USNM JAP 5249; 3.3 km ESE Cuyujúa, 2350 m, KU 143417-18, 146099; 6.6 km ESE Cuyujúa, Río Molando, 2360 m, KU 146098; 7 km E[SE]

Cuyujúa, 2195 m, USNM JAP 5351-57; 9 km E[SE] Cuyujúa, 2105 m, USNM JAP 5317-18; 1 km W Cuyujúa, 2500 m, USNM JAP 5308; 1.5 km W Cuyujúa, 2440 m, USNM JAP 5260-61; 2.5 km WNW Cuyujúa, 2550 m, KU 143419-30; 7.8 km WNW Cuyujúa, 2750 m, KU 143431; 4.6 km E[SE] Papallacta Río Papallacta (probably equals Chaspi Chico bridge), 2890 m, KU 143432-33; 11 km ESE Papallacta, 2660 m, KU 155442-47, 165435-67, 166273-74 (cleared and stained skeletons), 177286; 12 km ESE Papallacta, 2630 m, KU 165423-34, 166275-76 (cleared and stained skeletons); 13.1 km ESE Papallacta, 2610 m, KU 177287-90

Eleutherodactylus ignicolor (4 spec.)

ECUADOR, *Prov. Napo*: 9.2 km ESE Papallacta, 2750 m, KU 177296-97; 11 km ESE Papallacta, 2660 m, KU 165880; Río Jatuntinahua, 10 km SE Cuyujúa, 2160 m, KU 165879.

Eleutherodactylus incanus (22 spec.)

ECUADOR, *Prov. Napo*: Río Azuela, 1740 m, KU 143465-83; 16.5 km NNE Santa Rosa, 1700 m, KU 143457-58, 143460.

Eleutherodactylus incomptus (68 spec.)

ECUADOR, *Prov. Napo*: Río Azuela, 1740 m, KU 143497; Río Salado \pm 1 km upstream from Río Coca, 1410 m, KU 146169, 165844-58, 177298-319; 2 km SSW Río Reventador, 1490 m, KU 165932; 16.5 km NNE Santa Rosa, 1700 m, KU 143455, 143461-64, 143484-96; *Prov. Pastaza*: 9.5 km NW Mera, 1270 m, KU 179000-03.

Eleutherodactylus inusitatus (3 spec.)

ECUADOR, *Prov. Napo*: Agua Caliente on Río Pedro, SE of Cayambe, CAS-SU 8279; Río Jatuntinahua, 10 km SE Cuyujúa, 2160 m, KU 166066; *Prov. Pastaza*: Abitagua, 8 km NW Mera, 1300 m, KU 120099.

Eleutherodactylus lacrimosus (43 spec.)

Only Amazonian slope records are given below; see Lynch (1980) and Lynch and Schwartz (1972) for lowland records. 99 lowland specimens were also examined.

ECUADOR, *Prov. Pastaza*: Mera, 1140 m, KU 119513-17, 119522-23, 132631-32, 177361-68, 177376-82; Puyo, 960 m, KU 146100; 1 km N Puyo, 945 m, USNM 167372-78; 1 km W Puyo, 1000 m, MCZ 92030, 92037; Río Alpayacu, 1 km E Mera, 1100 m, KU 119518-21; 2 km S Shell Mera, 1006 m, USNM 167383-84; 3 km S Shell Mera, 960 m, USNM 167385-87.

Eleutherodactylus lanthanites (30 spec.)

Only specimens from the Amazonian slopes are

listed here; see Lynch (1975b, 1980) for lowland records. 431 lowland specimens also examined.

COLOMBIA, *Depto. Putumayo*: 10.3 km W El Pepino, 1440 m, KU 168834-45, 170172.

ECUADOR, *Prov. Napo*: Cerro Caleras (= Galeras), CAS-SU 10362; 7 km SW Río Azuela, KU 155448; 2 km SSW Río Reventador, 1490 m, KU 165885-93, 165931; *Prov. Pastaza*: 1 km W Puyo, 1000 m, MCZ 90037-48, 92034-35, 92128-30, 92132.

Eleutherodactylus leoni (65 spec.)

COLOMBIA, *Depto. Nariño*: La Victoria, 2700 m, KU 140311.

ECUADOR, *Prov. Carchi*: El Carmelo, 2715 m, USNM JAP 4951; 5.7 km NW El Carmelo, 2910 m, KU 177341-42; 14 km (airline) SE Maldonado, 2500 m, KU 177320-40; *Prov. Imbabura*: N slope Nudo de Mojanda, 3400 m, KU 130870-72; La Delicia, 2710 m, KU 132799; *Prov. Pichincha*: Palma Real, WCAB 35662; *Prov. Napo*: Santa Barbara, 2590 m, USNM 197941(6), 197944(11), GOV 7172-73, 7175, 7178, 7188, 7205, JAP 4482, 4484, 4486, 4541; 0.8 km NW Santa Barbara, Quebrada El Corazon, 2540 m, KU 177343; 1 km SW Santa Barbara, 2590 m, USNM 197942(4), JAP 4496, 4589; between Santa Barbara and Alegria, 2130-2440 m, USNM 197943.

Eleutherodactylus leucopus (32 spec.)

COLOMBIA, *Depto. Nariño*: La Victoria, 2700 m, KU 140303-07, 140312.

ECUADOR, *Prov. Napo*: Santa Barbara, 2590 m, USNM 197927-36, 197940(7), JAP 7192, 7194; 1 km NW Santa Barbara, 2590 m, USNM 197938(2); 1 km SW Santa Barbara, 2590 m, USNM 197939(2); 3 km SW Santa Barbara, 2440 m, USNM 197937.

Eleutherodactylus lividus (17 spec.)

ECUADOR, *Prov. Napo*: 4 km E Chalpi, 2590 m, USNM JAP 5554-55; 3 km E[SE] Cuyujúa, 2135 m, USNM JAP 5251; 9.2 km ESE Papallacta, 2750 m, KU 177344; 9.6 km E[SE] Papallacta, 2700 m, MCZ 92115; 11 km ESE Papallacta, 2660 m, KU 155450, 165935-36, 165937-40, 166005-07; 12 km ESE Papallacta, 2630 m, KU 165992, 166004.

Eleutherodactylus nigrogriseus
(46 spec.)

ECUADOR, *Prov. Morona-Santiago*: El Cruzado, 2195 m, USNM JAP 7283-86; Loma de Puerco, 2226 m, USNM JAP 7359-62; Pailas, 2195 m, USNM JAP 6663; San Vicente, 2835 m, USNM JAP 7653; Sapote, 2470 m, USNM JAP 7616-20; 2 km W Sapote, 2561 m, USNM JAP 7656; *Prov. Napo*: S slope Cor-

dillera del Dué above Río Coca, 1150 m, KU 123501; *Prov. Pastaza*: Abitagua, 1330 m, KU 120157-63, 120164(2); 3.5 km W Mera, 1180 m, KU 146109-11; 8.1 km NW Mera, 1270 m, KU 177345-48; 9.5 km NW Mera, 1270 m, KU 177349-55; *Prov. Tungurahua*: Baños, NHRM 1905(6).

Eleutherodactylus nigrovittatus
(82 spec.)

Only specimens from the Amazonian slopes are listed here; see Lynch (1980) for lowland records. 49 lowland specimens also examined.

ECUADOR, *Prov. Morona-Santiago*: Río Yuquipa, Macas, USNM GOV 7210; *Prov. Napo*: S slope Cordillera del Dué above Río Coca, 1150 m, KU 123503-42, 123544-65; La Bonita, 1935 m, USNM JAP 4831; slopes of Mt. Sumaco, AMNH 22284, 22287-89, 22293-98, 22327, 22335-37, USNM GOV 8899-900; *Prov. Pastaza*: Mera, 1100 m, KU 177356-57.

Eleutherodactylus ockendeni (11 spec.)

Only Amazonian slope specimens are listed below; see Lynch (1974, 1980) for lowland records. 314 lowland specimens were also examined.

ECUADOR, *Prov. Napo*: S slope Cordillera del Dué above Río Coca, 1150 m, KU 123809-11; *Prov. Pastaza*: Mera, 1140 m, KU 120261, 120269, 177358-59.

PERÚ, *Depto. Huánuco*: S slope Serranía Sira, Laguna, 1280 m, KU 154783-85; S slope Serranía Sira, Pata Rojo, 1100 m, KU 154782.

Eleutherodactylus pastazensis (4 spec.)

ECUADOR, *Prov. Tungurahua*: Runtún (Baños), CAS-SU 5084; Volcán Tungurahua, 1840 m, NHRM 1918 (small specimen); Yanguilla, CAS-SU 5065, NHRM 1918 (larger individual).

Eleutherodactylus peruvianus (52 spec.)

Only specimens from the Amazonian slopes are listed below; see Lynch (1980) for lowland records. 346 lowland specimens were also examined.

ECUADOR, *Prov. Morona-Santiago*: Río Piúntza, Cordillera del Condor, 1830 m, KU 147034-38; Pastaza River, Canelos to Marañon, MCZ 19635-36, 19639, 89314; *Prov. Napo*: "top" of Mt. Sumaco, AMNH 22202-04; 3.2 km NNE Oritoyacu, 1910 m, KU 177360; Río Azuela, 1740 m, AMNH 89743-48, KU 143502-03; Río Salado \pm 1 km upstream of Río Coca, 1410 m, KU 165859-65; 16.5 km NNE Santa Rosa, 1700 m, KU 143498-501; *Prov. Pastaza*: Mera, 1000 m, UMMZ 92124; near Mera, 1000 m, UMMZ 92126(5); *Prov. Tungurahua*: Abitagua, 1100-1200 m, CAS-SU 5070, 5079, UMMZ 92119(2), 92120, 92121(3); El Topo,

UMMZ 51264. *Province unknown*: Mapoto, 1300 m, UMMZ 89069.

PERÚ, *Depto. Jujín*: Valle de Perene, 1500 m, AMNH 38598-601.

Eleutherodactylus petersi (71 spec.)

COLOMBIA, *Depto. Huila*: Parque Arqueológico San Agustín, 1750 m, KU 168818-22; *Depto. Putumayo*: 10.3 km W El Pepino, 1440 m, KU 168812; 35 km SE San Francisco, 1950 m, KU 168813-17.

ECUADOR, *Prov. Napo*: La Bonita, 1935 m, USNM JAP 4637; 2 km SE La Bonita, 1920 m, USNM 204704, JAP 4862-68, 4870-80; Loreto, USNM JAP 9367-68; Río Azuela, 1740 m, KU 143506-07, 165993; Río Salado, \pm 1 km upstream from Río Coca, 1410 m, KU 165994-6003, 177383; 16.5 km NNE Santa Rosa, 1700 m, KU 143508-12; *Prov. Pastaza*: Mera, 1140 m, KU 120247-49, 177369-75; *Prov. Tungurahua*: Baños, 1829 m, USNM JAP 5840-47; Río Blanco, UMMZ 92136; Yanguilla, UMMZ 92138.

Eleutherodactylus prolatus (91 spec.)

ECUADOR, *Prov. Napo*: S slope Cordillera del Dué above Río Coca, 1150 m, KU 123755-61; 2 km SSW Río Reventador, 1490 m, KU 166008-15; Río Salado, 1 km upstream from Río Coca, 1410 m, KU 146163, 146165-68, 166016-30, 177384-438; *Prov. Pastaza*: Mera, 1140 m, KU 120176.

Eleutherodactylus proserpens (27 spec.)

ECUADOR, *Morona-Santiago Prov.*: El Cruzado, 2195 m, USNM 199751; Plan de Milagro, 1707 m, USNM 198485, 198504; 1 km S Plan de Milagro, 1707 m, USNM 198503; Río Piúntza, Cordillera del Condor, 1830 m, KU 147044-46; 1/2 km E Sapote, 2393 m, USNM 199752; 1 km E Sapote, 2332 m, USNM 198499-501, 199753; mountain above Sapote (to the south), 2500 m, USNM 198496-98; 1/2 km W Sapote, 2546 m, USNM 198486-91; between Sapote and Suro Rancho, 2622 m, USNM 198484, 198492-95, 198502.

Eleutherodactylus pugnax (9 spec.)

ECUADOR, *Prov. Napo*: Río Azuela, 1740 m, EP 70/978, KU 155449; Río Jatuntinahua, 10 km SE Cuyujúa, 2160 m, KU 165561-62; Salto de Agua, 2.5 km NNE Río Reventador, 1660 m, KU 146466-67; 0.5 km NW Santa Barbara, 2540 m, KU 177440-41; 3.7 km NW Santa Barbara, 2410 m, KU 177439.

Eleutherodactylus pycnodermis
(137 spec.)

ECUADOR, *Azuay Prov.*: 3 km E Sevilla de Oro, 2713 m, USNM 199851-53; 5 km ESE

Sevilla de Oro, 2957 m, USNM 199854, 199867; between Sevilla de Oro and Cerro Negro, 3110 m, USNM 199868; crest at Azuay-Morona Santiago frontier, ca. 8 km SE Sevilla de Oro, 3354 m, USNM 199855-59, 199866; crest at Azuay-Morona Santiago frontier, ca. 8 km SE Sevilla de Oro, 3384 m, USNM 199758-59, 199860-65. *Morona-Santiago Prov.*: between Cerro Negro and Pailas, 2652 m, USNM 199755-57, 199869-71; San Vicente, 2805-35 m, USNM 199754, 199815-50, 199884, 199888-90; San Vicente, 2851 m, USNM 199813-14, 199885-87; 3 km W San Vicente, 2988 m, USNM 199794-812, 199882-83; 6 km W San Vicente, 3100 m, USNM 199787-93, 199880-81; Suro Rancho, 2683 m, USNM 199760-66; 1/2 km W Suro Rancho, 2744 m, USNM 199767-86, 199872-79.

Eleutherodactylus quaquaversus
(176 spec.)

ECUADOR, *Prov. Morona-Santiago*: Cusume, Río Cusume, 320 m, AMNH 93646; Río Piúntza, Cordillera del Condor, 1830 m, KU 146987-90; *Prov. Napo*: Bermejo No. 4 (well site), 15 km ENE Umbaqui, 740 m, KU 123690-701; S slope Cordillera del Dué above Río Coca, 1150 m, KU 123731-53; Loreto, USNM GOV 9371-72, 9557, JAP 9199, 9204; side of Mt. Sumaco, AMNH 22338; Puerto Libre, Río Aguarico, 570 m, KU 123706-30, 123778-80; Quebrada Pacayacu, tributary of Río Cotapino, 600-650 m, CAS-SU 13153; Río Azuela, 1740 m, KU 143448-54; 2 km SSW Río Reventador, 1490 m, KU 165563-65; Río Salado, \pm 1 km upstream from Río Coca, 1410 m, KU 165566-85, 166281-82 (cleared and stained skeletons); Santa Cecilia, 340 m, KU 104593-96, 111181, 123702-05, 146161, 149197-99, 149232-37; 16.5 km NNE Santa Rosa, 1700 m, KU 143441-47; *Prov. Pastaza*: Mera, 1140 m, KU 120165, 120169, 177442-50; Puyo, 960 m, UMMZ 164323; 3 km S Puyo, 920 m, KU 127034, 1 km W Puyo, 1000 m, MCZ 90116-38; Río Alpayacu, 1 km E Mera, 1100 m, KU 120166-68, 120170-72; headwaters, Río Bobonaza, 685 m, USNM JAP 2131; Shell Mera, UIMNH 93562; 10 km ESE Veracruz, MCZ 90139.

Eleutherodactylus rubicundus (19 spec.)

ECUADOR, *Prov. Napo*: S slope Cordillera del Dué above Río Coca, 1150 m, KU 123754, 123762-64; *Prov. Pastaza*: Abitagua, 1100 m, CAS-SU 5077; Abitagua, 1200 m, UMMZ 92115; Abitagua, 8 km NW Mera, 1300 m, KU 120173; Mera, 1140 m, KU 177452-56, UMMZ 92116; 9.5 km NW Mera, 1270 m, KU 177457-58; 5 km E, 6 km S Puyo, 925 m, MCZ 92027; Río Alpayacu, 1 km E Mera, 1100 m, KU 120174-75; *Prov. Tungurahua*: 11 km E Río Negro, 1170 m, KU 146170.

Eleutherodactylus spinosus (100 spec.)

ECUADOR, *Morona-Santiago Prov.*: between Cerro Negro and Pailas, 2652 m, USNM 199916; between Cerro Negro and Pailas, 2439-2561 m, USNM 199917; El Cruzado, 2195 m, USNM 199945-66; Loma de Puerco, 2226 m, USNM 199967-71; Pailas, 2195 m, USNM 199918-35, 199973-77; 1 km S Plan de Milagro, 1707 m, USNM 199978; Río Piúntza, Cordillera del Condor, 1830 m, KU 147039; San Juan Bosco, 2195 m, USNM 199936-44, 199979-82; San Vicente, 2835 m, USNM 199972, 199988-89; Sapote, 2470 m, USNM 199891-915, 199986-87; between Sapote and Suro Rancho, 2604-2622 m, USNM 199983-85.

Eleutherodactylus trachyblepharis
(79 spec.)

ECUADOR, *Prov. Morona-Santiago*: Cusume, Río Cusume, 320 m, AMNH 93668-69; *Prov. Pastaza*: Abitagua, 1200 m, UMMZ 92117(2), 92118; Abitagua, 8 km NW Mera, 1300 m, KU 120199-200; Canelos, 530 m, KU 120253; Mera, 1140 m, KU 120179-80, 120182-98, 120205-09, 120210(2), 120442, 177458-68; Puyo, 1000 m, USNM JAP 6184; 5 km SSE Puyo, 975 m, USNM JAP 2022, 2024; 5 km E, 6 km S Puyo, 925 m, MCZ 92022-26; 1 km W Puyo, 1000 m, MCZ 92029; Río Alpayacu, 1 km E Mera, 1080-1100 m, KU 120181, 120204; Sarayacu, 400 m, KU 120254; Veracruz, 950 m, KU 120203, USNM JAP 6145, 6147; 10 km ESE Veracruz, MCZ 90143-44; *Prov. Tungurahua*: El Topo, 1280 m, BM 1912.11.1.58-60 (re-registered as 1947.2.17.2-4); Río Negro, 1260 m, KU 120211-14, USNM JAP 6075, 6077, 6079-81, 6083-87.

Eleutherodactylus trepidotus (112 spec.)

ECUADOR, *Prov. Napo*: Cuyujúa, 2360 m, USNM JAP 5214-15, 5609-14; 2.5 km WNW Cuyujúa, 2550 m, KU 143434; Laguna de Papallacta, 3330 m, KU 143435-40; Laguna del San Marcos, NE of Cayambe, CAS-SU 8300; Llanganati mountains, El Golpe, 3000 m, CAS-SU 13191-92, 17428; Papallacta, BM 1926-12.4.1 (re-registered as 1947.2.15.47), MSNT 428(9), 819, UIMNH 55869-91 (55874 cleared and stained skeleton), 55916-17; 3.4 km ESE Papallacta, Quebrada San Pedro, 2960 m, KU 177882; 1 km W Papallacta, 3155 m, KU 106938-42, USNM 160940-43, 160945-46, 106948-49, 160951-53, 106960, 106962-65, 106969, 164399-406, JAP 5153-54; 2 km W Papallacta, 3270 m, KU 177883-87; 4 km W Papallacta, 3300 m, KU 117618-22, 118134-35 (cleared and stained skeletons); 4.7 km W Papallacta, 3360 m, KU 177881; 5 km W Papallacta, 3250 m, USNM 164407-11; east slope, Paso de Guamaní, 3650 m, KU 109061-63; Río Bermejo, Cordillera de Guacamayo, KU

106937, WCAB 35641; *Prov. Tungurahua*: 10 km W Baños, 2925-3050 m, USNM JAP 5860.

Eleutherodactylus unistrigatus
(29 spec.)

Only specimens from the Amazonian slopes are listed below; Lynch (ms) will report highland material later. More than 1300 highland specimens were also examined.

COLOMBIA, *Depto. Putumayo*: Colón, 2220 m, KU 168618-24; 4 km SE San Francisco, 2320 m, AMNH 84837-38.

ECUADOR, *Prov. Carchi*: El Carmelo, 2710 m, KU 177521-28; 5.7 km NW El Carmelo, 2910 m, KU 177529-32; *Prov. Napo*: ca. 25-30 km SE Cayambe, 3200 m, CAS-SU 8280; Santa Barbara, USNM GOV 7183, 7200, 7207; *Prov. Tungurahua*: Baños, 1900 m, CAS-SU 5083, KU 141379-80, UIMNH 55722.

Eleutherodactylus ventrimarmoratus
(31 spec.)

ECUADOR, *Prov. Morona-Santiago*: Ashura village on Río Macuma, 300 m, AMNH 94685-86; General Plaza, 1100 m, USNM JAP 6954, 6956; Miazal, USNM GOV 9657; *Prov. Napo*: Loreto, USNM GOV 9364-65, JAP 3854; Río Azuela, 1740 m, EP 68/976; *Prov. Pastaza*: Abitagua, 1100 m, CAS-SU 5078, UMMZ 92131-33; Abitagua, 8 km NW Mera, 1300 m, KU 119810-11; Mera, 1140 m, KU 119805-06, 119809; near Mera, 1000 m, UMMZ 92127; Río Alpayacu, 1 km E Mera, 1100 m, KU 119807-08; *Prov. Tungurahua*: El Topo, 1280 m, BM 1911.1.151-53 (reregistered as 1947-2.1574-76).

PERÚ, *Depto. Amazonas*: headwaters of Río Caterpisa, Manseriche range, 457 m, AMNH 42435; *Depto. Huánuco*: Finca Panguana, Río Lullapichis, 4-5 km upstream from Río Pachitea, 200 m, KU 154801; *Depto. Junín*: Chanchamayo, BM 1911.12.12.77 (reregistered as 1947.2.1573); *Depto. Loreto*: Río Utoquinia, AMNH 43376; Tipishca, opposite Contamana, AMNH 42938; *Depto. Madre de Dios*: Cocha Cachu, Río Manú between Río Cachiri and Río Panagua, 400 m, KU 154803; Manú, 365 m, KU 154802.

Eleutherodactylus w-nigrum
(377 spec.)

Only specimens from the Amazonian slopes are listed below. 1444 other examples have been examined from Colombia and Ecuador.

COLOMBIA, *Depto. Cundinamarca*: east base of Cordillera de Bogotá, ANSP 24394; *Depto. Putumayo*: 10.3 km W El Pepino, 1440

m, KU 168735-41; Mocoa, CAS 85176; ca. 15 km (airline) SW Mocoa, 1180-1480 m, AMNH 84851-52; 4 km (airline) SE San Francisco, 2320 m, AMNH 84839-46; 35 km SE San Francisco, 1950 m, KU 168721-34.

ECUADOR, *Prov. Morona-Santiago*: Agua Rica, 1890 m, USNM JAP 7072; El Cruzado, 2195 m, USNM JAP 7209-17; Gallineros, 2195 m, USNM JAP 7226-27; Loma de Puerco, 2226 m, USNM JAP 7334-47, 7358; between Loma de Puerco and Sapote, 2317-2408 m, USNM JAP 7401-05, 7322-33; Pailas, 2195 m, USNM JAP 6546-53, 6662, 6675-81, 6725, 6777-93; between Pailas and Mirador, 1982-2195 m, USNM JAP 6705, 6707-10; San Juan Bosco, 2195 m, USNM JAP 7066-69, 7083-86, 7088, 7223-25; slightly downtrail from San Juan Bosco, 2113 m, USNM JAP 7256-59; slightly downtrail from San Juan Bosco, 2192 m, USNM JAP 7229-33; between San Juan Bosco and El Cruzado, 2226 m, USNM JAP 7177-91, 7193-96; Sapote, 2470 m, USNM JAP 7507-11, 7542-60; 1 km W Sapote, 2564-2591 m, USNM JAP 7411-16; between Sapote and Suro Rancho, 2604 m, USNM JAP 7762; *Prov. Napo*: Alto Río Quijos, El Chaco, 1600 m, USNM GOV 8007; Baeza, 1870 m, KU 146063-64, USNM JAP 5728-29; Borja, 1707 m, USNM JAP 5386, 5437, 5442; 6.6 km ESE Cuyujúa, Río Molando, 2360 m, KU 146066-70; 7 km E[SE] Cuyujúa, 2195 m, USNM JAP 5207, 5359; 9 km E[SE] Cuyujúa, 2104 m, USNM JAP 5219, 5319; La Alegria, 1900 m, USNM JAP 4608-09, 4621-22, 4626-28, 4662-63, 4665-80, 4718-19, 4721-30, 4732-48, 4848-57, 4897-99; La Bonita, 1650 m, USNM JAP 4715-17, 4858-60, 4915; Loreto [probably in error], USNM GOV 7090; 3.2 km NNE Oritoyacu, 1910 m, KU 177568-81; Papallacta, WCAB 37923, 37930; Río Azuela, 1740 m, KU 143303-16, 165659-62; Río Jatuntinahua, 2160 m, KU 165683-88; 2 km SSW Río Reventador, 1490 m, KU 165663-80, 166286 (cleared and stained skeleton); Río Salado, 1 km upstream from Río Coca, 1410 m, KU 146065, 165681-82, 177582-91; Santa Barbara, 2591 m, USNM GOV 8542-43, 8545, JAP 4542-54, 4556; 0.5 km NW Santa Barbara, 2540 m, KU 177592; 1 km SW Santa Barbara, 2591 m, USNM JAP 4586-87; between Santa Barbara and L'Alegria, 2134-2439 m, USNM JAP 4592-96; 16.5 km NNE Santa Rosa, 1700 m, KU 143301-02; between Sebunday and La Bonita, 1524-1829 m, USNM JAP 4630-31; *Prov. Pastaza* [probably in error]: Río Villano, USNM JAP 6257-59, 6261-62; *Prov. Tungurahua*: Abitagua, 1100 m, UMMZ 92119 (one individual); 18.5 km E Baños, 1600 m, KU 141291; *Prov. Zamora-Chinchi*: 23 km E Loja, 2220 m, KU 141966.

APPENDIX B: GAZETTEER

Following is a list of localities on the eastern slopes of the Andes where specimens of *Eleutherodactylus* were collected. After each place name the province is given in parentheses, followed by geographic coordinates and elevation. Coordinates were determined from the 1974 Edition of Mapa de Ecuador, Instituto Geográfico Militar, Quito (1:1,000,000). Most of the elevations were determined from altimeter readings at the sites. When known, specific sites and habitats are given, followed by names of collectors and months and years that they collected at the sites. Names of some collectors are abbreviated: JAP = James A. Peters, JDL = John D. Lynch, WED = William E. Duellman.

Abitagua (Pastaza)—01°26' S, 78°07' W, 1300 m. Region on Baños-Puyo road in Pastaza Trench, 8 km NW of Mera. Small streams in lower montane rainforest. Wm. Clarke-MacIntyre, Sep. 1939; JDL, Jul. 1968, Jul. 1977. 32

Agua Caliente (Napó)—00°22' S, 77°52' W, ≈ 3000 m. Place on the Río San Pedro, a tributary of the upper Río Azuela on the eastern slope of Volcán Cayambe. I. L. Wiggins, Jul. 1944. 5

Alpayacu, Río (Pastaza)—01°28' S, 78°05' W, 1100 m. Small tributary of Río Pastaza, 1 km E Mera; remnants of lower montane rainforest. Wm. Clarke-MacIntyre, Sep. 1939; JDL, Jul. 1968, Jul. 1977. 34

Azuela, Río (Napó)—00°07' S, 77°37' W, 1740 m. Tributary of Río Coca east slope of Volcán Cayambe. Collections from slopes above (NW) of point where Papallacta-Lago Agrio road crosses river; lower montane rainforest (1971), partly cultivated in *naranjilla* (1974). WED, Oct. 1971, Oct. 1974, Mar. 1975; C. W. Myers, Feb. 1974; F. Ortiz C., Jan. 1976. 8

Baeza (Napó)—00°28' S, 77°53' W, 1990 m. Town on bluff just southwest of confluence of Río Papallacta and Río Cosanga to form Río Quijos. Collections from vicinity of town in partly cleared lower montane rainforest; many large trees with abundant bromeliads. JAP, Jul. 1962; WED, Oct. 1971, Apr. 1972. 17

Baños (Tungurahua)—01°23' S, 78°24' W, 1800 m. Town in upper part of Pastaza Trench; dry subtropical forest. Collections from vicinity of town and valley (many labelled only as "Baños") by Wm. Clarke-MacIntyre Jul. 1937, and Olallas, 1932-43; WED, Jul. 1971, Apr. 1972. Collections in partly cleared lower montane rainforest, 8.4 km E of Baños, 1590 M, WED, Apr. 1972. Collections from grazed subalpine woodland, 10 km W of Baños, 3000 m, WED, Jul. 1972. 27

Bermejo, Río (Napó)—00°31' S, 77°53' W, 1910 m. River draining north slope of Cordillera de Guacamayo; Baeza-Tena road crosses river 12.5 km S of Baeza, at settlement

of Bermejo at junction of Río Bermejo and Río Cosanga. 19

Borja (Napó)—00°25' S, 77°51' W, 1710 m. Village just west of Río Quijos, just off of Papallacta-Lago Agrio road; mostly cleared lower montane rainforest with scattered large trees in pastures. JAP, Jul. 1962. 15

Cerro Negro (Azuay)—02°45' S, 78°32' W, 2925 m. Place just east of Sevilla de Oro on trail to Méndez; subalpine rainforest. JAP, Aug. 1962. 39

Chalpi (Napó)—00°23' S, 78°04' W, 2590 m. Finca 8.3 km ESE of Papallacta on road to Lago Agrio; pastures amidst remnants of upper montane rainforest, JDL, Jul. 1977. Collections from short distances east and west, JAP, Jul. 1962. 13

Cutucú, Cordillera (Morona-Santiago)—≈ 02°45' S, 78°05' W, 2000+ m. Isolated mountain range east of Méndez. E. Feyer, 1921. 41

Cuyujúa (Cuyuja) (Napó)—00°24' S, 78°02' W, 2460 m. Small village 17 km ESE of Papallacta on road to Lago Agrio. Pastures with remnants of upper montane rainforest in ravines. Collections from vicinity of village, JAP, Jul. 1962; from 7.8 km WNW (2750 m), 3 km E (2135 m), Río Victoria, 1 km E (2420 m), and Río Molando, 6.6 km ESE (2360 m), WED, Oct. 1971, Apr. 1972. 14

Dué, Cordillera del (Napó)—00°03' S, 77°35' W, 1150 m. Ridge between Río Coca (S) and Río Dué (N); lower montane rainforest. WED, Aug. 1968. 6

El Carmelo (El Pun) (Napó)—00°40' N, 77°37' W, 2750 m. Small town on upper Río Chingual; patches of upper montane rainforest in otherwise cultivated areas; JAP, Jun. 1962; JDL, Jul. 1977. Same habitat at 5.7 km NW of El Carmelo on road to Tulcán; JDL, Jul. 1977. 1

El Cruzado (Morona-Santiago)—03°03' S, 78°31' W, 2195 m. Ranch on trail from Gualaico to General Plaza, 0.5 hr up trail from San Juan Bosco; "montane forest"; JAP, Aug. 1962. 49

El Golpe (Napó)—01°10' S, 78°20' W, 3000 m. Place name (along Río El Golpe?) on higher eastern slope of Los Llanganatis. R. Blomberg, Dec. 1951. 25

El Topo (Tungurahua)—01°25' S, 78°10' W, 1220 m. Settlement 32 km E of Baños on road to Puyo; lower montane rainforest, citrus groves, and pasture. M. G. Palmer, 1912. 30

General Plaza (Morona-Santiago)—02°58' S, 78°26' W, 1100 m. Town on Río Yunganza; lower montane rainforest. JAP, Aug. 1962. 43

Jatúntinahua (Jatún Tinajua), Río (Napó)—00°26' S, 77°57' W, 2160 m. Tributary of Río Papallacta, 27.2 km ESE of Papallacta on road to Lago Agrio; upper montane rainforest and pasture. WED, Apr. 1975. 16

Jorge, Río (Napó)—≈ 01°08' S, 78°17' W,

3000 m. Stream on high eastern slopes of Los Llanganatis. R. Blomberg, Dec. 1951. 24

La Alegría (Napó)—00°33' N, 77°31' W, 1930 m. Settlement on Río Chingual, 20 km N of La Bonita. Presumably lower montane rainforest. JAP, Jun. 1962. 3

La Bonita (Napó)—00°29' N, 77° 32' W, 1920 m. Small village on Río Chingual; presumably lower montane rainforest. JAP, Jun. 1962. 4

Loma de Puerco (Morona-Santiago)—03° 02' S, 78°32' W, 2225 m. Rancho between Sapote and El Cruzado on Gualaceo-General Plaza trail. JAP, Aug. 1962. 45

Los Llanganatis (Tungurahua, Napó)—≈ 01°10' S, 78°12' W, 4000+ m. A highland region immediately to the north of the Pastaza Trench. R. Blomberg, Dec. 1950, Dec. 1951. 26

Macas (Morona-Santiago)—02°19' S, 78° 07' W, 1015 m. Town on Río Upano in foothills of Andes. Cultivated with few remnants of rainforest. Olallas. 36

Méndez (Morona-Santiago)—02°43' S, 78° 19' W, 550 m. Town on the lower Río Paute. Collections from various elevations between Méndez and Sevilla de Oro (2550 m). JAP, Aug. 1962. 37

Mera (Pastaza)—01°28' S, 78°06' W, 1000 m. Town in lower Pastaza Trench, 18 km WNW of Puyo on road to Baños. Cultivated with remnants of rainforest in ravines and on steep slopes N of town; JDL, Jul. 1968, Jul. 1977. Collections from forested ravines 6.6 km NW (1200 m), 8.1 km NW (1270 m), and 9.5 km NW (1270 m) of Mera on road to Baños; WED, Apr. 1972. 33

Mirador (Morona-Santiago)—02°44' S, 78° 22' W, 1982 m. Rancho on Sevilla de Oro-Méndez trail. JAP, Aug. 1962. 38

Mirador (Tungurahua)—01°26' S, 78°15' W, 1530 m. Finca on N slope of Río Pastaza, 8.4 km E of Baños on road to Puyo. Second growth lower montane rainforest and cultivated fields. Olallas, P. O. Simons, 1899. 31

Oritoyacu (Napó)—00°29' S, 77°52' W, 1910 m. Settlement at crossing of Baeza-Tena road of Río Oritoyacu, 10.1 km S of Baeza. Collections from Quebrada Amarilla, 3.2 km NNE Oritoyacu; lower montane rainforest. JDL, Jul. 1977. 18

Pailas (Azuay)—02°45' S, 78°31' W, 2195 m. Rancho on Sevilla de Oro-Méndez trail. JAP, Aug. 1962. 40

Papallacta (Napó)—00°20' S, 78°05' W, 3150 m. Village near headwaters of Río Papallacta; subalpine rainforest. Collections from immediate vicinity of village; JAP, Jul. 1962, JDL, Jul. 1967, Feb. 1968, Jul. 1977; WED, Mar. 1967, Oct. 1971. Collections from Quebrada San Pedro, 3.4 km ESE (pastures), JDL, Feb. 1968, Jul. 1977; upper montane rainforest and pastures, 9.2 km ESE, JDL, Jul. 1977;

11-12 km ESE, R. Altig, Dec. 1973, Jan. 1974; WED, Oct. 1974, Mar.-Apr. 1975; Finca Santa Fe, 13.1 km ESE, JDL, Jul. 1977. 12

Paracayacu (Río Paracayacu ?) (Napó)—01° 07' S, 78°15' W, 2700 m. Stream on high eastern slope of Los Llanganatis. R. Blomberg, Dec. 1951. 23

Piuntza, Río (Morona-Santiago)—03°52' S, 78°27' W, 1830 m. Stream on western slope of northern part of Cordillera del Condor, flowing into Río Zamora about 30 km SSW of Yuquianza. Collections from upper montane rainforest near crest of cordillera. J. E. Simons, Jan. 1972. 51

Plan de Milagro (Morona-Santiago)—03° 03' S, 78°29' W, 1710 m. Rancho about 10 km WSW of General Plaza on trail to Gualaceo. JAP, Aug. 1962. 50

Puyo (Pastaza)—01°29' S, 77°59' W, 1000 m. Town in Andean foothills; pastures, citrus groves, and tea plantations. Olallas; JAP; WED, Apr. 1972. 35

Reventador, Río (Napó)—00°07' S, 77°38' W, 1490 m. Tributary of Río Coca draining south slope of Volcán Reventador. Collections from vicinity of two small streams, 2 km WSW of Puente Reventador on Papallacta-Lago Agrio road; lower montane rainforest on steep slopes. R. Altig, Dec. 1973; WED, Oct. 1974, Mar. 1975. 7

Río Negro (Tungurahua)—01°25' S, 78°13' W, 1240 m. Village in Pastaza Trench, 29.7 km E of Baños on road to Puyo. Collections in secondary forest and abandoned *naranjilla* plantations in immediate vicinity of village; JDL, Jul. 1968. Collections from citrus groves and extensively disturbed lower montane rainforest 11 km E of village (1170 m); WED, Apr. 1972. 29

Runtún (Tungurahua)—≈01°24' S, 78°35' W, 1840 m. Northeast shoulder of Volcán Tungurahua, south of Baños. Wm. Clarke-MacIntyre, Jun. 1939. 28

Sabanilla (Zamora-Chinchipec)—03°57' S, 79°03' W, 1750 m. Village on Loja-Zamora road. Badly cutover lower montane rainforest. H. E. Anthony, Nov. 1920. 52

Salado, Río (Napó)—00°13' S, 77°44' W, 1410 m. River draining east slope of Volcán Cayambe. Collections made in vicinity of small settlement of Río Salado at point where Papallacta-Lago Agrio road crosses Río Salado, about 1 km upstream from its confluence with the Río Coca; lower montane rainforest with swamp and many small streams. WED, Apr. 1972, Oct. 1974, Mar. 1975; JDL, Jul. 1977. 10

Salto de Agua (Napó)—00°08' S, 77°38' W, 1660 m. Waterfall on Papallacta-Lago Agrio road, 2.5 km NNE of Puente Reventador; upper montane rainforest. WED, Apr. 1972. 9

San José (Napó)—00°36' S, 77°35' W, 1000 m. Finca owned by Olalla family on

lower eastern slopes of Volcán Sumaco. Olallas, 1920's-1950's. 21

San José, Río (Napo)— $01^{\circ}07' S$, $78^{\circ}15' W$, 3000 m. Stream on high eastern slopes of Los Llanganatis. R. Blomberg, Nov. 1950. 22

San Juan Bosco (Morona-Santiago)— $03^{\circ}03' S$, $78^{\circ}31' W$, 2195 m. Rancho on Gualaceo-General Plaza trail. JAP, Aug. 1962. 48

Santa Bárbara (Napo)— $00^{\circ}35' N$, $77^{\circ}33' W$, 2625 m. Town on upper Río Chingual. Upper montane rainforest and pastures (1962), but essentially cleared (1977). Collections from vicinity of town; JAP, Jun. 1962; JDL, Jul. 1977. Collections from 3.7 km NW of Santa Bárbara on road to Tulcán (2410 m); JDL, Jul. 1977. 2

Santa Rosa (Napo)— $00^{\circ}18' S$, $77^{\circ}43' W$, 1600 m. Village on Río Santa Rosa just upstream from Río Coca, 61 km from Papallacta on road to Lago Agrio. Collections from 16.5 km by road NNE of Santa Rosa, 1700 m; lower montane rainforest on upper slopes of Río Salado valley; WED, Oct. 1971. 11

San Vicente (Morona-Santiago)— $03^{\circ}02' S$, $78^{\circ}33' W$, 2835 m. Rancho on Gualaceo-General Plaza trail; subalpine rainforest. JAP, Aug. 1962. 44

Sapote (Morona-Santiago)— $03^{\circ}02' S$, $78^{\circ}32' W$, 2470 m. Rancho on Gualaceo-General

Plaza trail; patches of upper montane rainforest amidst pastures. JAP, Aug. 1962. 47

Sevilla de Oro (Azuay)— $02^{\circ}47' S$, $78^{\circ}34' W$, 2650 m. Village on upper Río Negro on trail from Paute to Méndez; collections from various elevations between Sevilla de Oro and Méndez. JAP, Aug. 1962. 42

Sumaco, Cerro (Napo)— $00^{\circ}35' S$, $77^{\circ}37' W$, 3900 m (crest). Isolated volcano rising from Andean foothills. Olallas, 1920's-1950's. 20

Suro Rancho (Morona-Santiago)— $03^{\circ}02' S$, $78^{\circ}32' W$, 2745 m. Rancho on Gualaceo-General Plaza trail. JAP, Aug. 1962. 46

Zamora (Zamora-Chinchipec)— $04^{\circ}05' S$, $78^{\circ}57' W$, 1000 m. Town in Río Zamora valley. Collections from extensively cleared lower montane rainforest on eastern slope of Andes, 22 km NW of Zamora on road to Loja (1730 m). WED, Jul. 1971. 54

Zamora, Abra de (Zamora-Chinchipec)— $04^{\circ}00' S$, $79^{\circ}07' W$, 2800 m. Crest of Cordillera Oriental, 13.5 km E of Loja on road to Zamora; also known as Nudo de Sabanilla. Subalpine forest with many large bromeliads on low bushes; JDL, Jun. 1968, Jan. 1978; WED, Jul. 1971, Mar. 1975. Collections from eastern slope, 15 km E of Loja (2710 m); WED, Jul. 1971; 23 km E Loja (2220 m); WED, Jul. 1971. 53